

A BIOLOGIC *and* PHYLOGENETIC STUDY
of the STROMATIC SPHAERIALES

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INTRODUCTION

Taxonomy should be an expression of phylogeny. A knowledge of the phylogeny of any group of organisms, however, must lag behind the necessity of its classification. The mere existence of a number of described species calls for a taxonomic system. A knowledge of the phylogenetic relationships comes only after a close scrutiny of the structure and development of these species. For this reason the first systems of classification of any group are necessarily artificial.

This is the case with the ascomycetous fungi. The enormous number of described species has necessitated the erection of systems of classification which are based upon arbitrarily chosen characters, resulting in a high degree of artificiality. Lindau (79) has long since pointed out that the only way to bring order to this mass of unassimilated species is to desist from the wholesale formation of species and to proceed to a study of the life histories of the forms already known.

The problem here undertaken is the determination of the phylogenetic relationships existing among certain ascomycetes, and the presentation of the outlines of a possible classification upon such a basis. In undertaking such a problem it is necessary to have, first of all, a thorough knowledge of the complete life histories of a large and representative number of species. This is especially true of the ascomycetes on account of their complicated life histories, which include two or more modes of spore-formation. In order to make this possible, the study is here limited to a reasonably well-defined group, the stromatic Sphaeriales. Since the only dependable method of determining the genetic connections of the various spore forms belonging to a given life history is by pure-culture methods, the life histories of a number of closely related forms of the stromatic Sphaeriales have been worked out in culture by the writer (127, 128, 129, 130). In the following pages an attempt will be made to correlate the results of these

¹ Papers from the Department of Botany of the University of Michigan, no. 238.

investigations, together with what other data are available, into a unified whole as regards the general developmental morphology and phylogenetic relationships of this group.

This work has been done at the cryptogamic laboratory of the University of Michigan under the direction of Dr. C. H. Kauffman, to whom I wish to express my extreme gratitude for the suggestion of the problem and the continual helpful supervision of the work.

HISTORICAL

The study of the fungi was much later in its development than that of the higher plants. The earlier writers had very vague ideas of the cryptogams, and generally supposed them to arise by spontaneous generation. As in the study of the higher plants, the work of the earlier mycologists, such as Persoon (87) and Fries (34), was mainly descriptive. The collectors of the earlier part of the nineteenth century described an enormous number of species, which were assembled in highly artificial systems of classification. A comprehensive knowledge of the fungi did not begin to develop until the middle of the nineteenth century, when the perfection of the microscope made minute microscopic studies possible and the researches of Hofmeister focused attention upon the lower cryptogams.

When the earlier systems of classification of the fungi were erected, the knowledge of the spore and its morphology was very slight, and as a result separations were based mainly on the gross morphological characters. In the Sphaeriales, the character and position of the perithecium and the configuration of the stroma became the chief diagnostic characters.

In 1851, a great stimulus was given to the study of the ascomycetes in general by the discovery, by L. R. Tulasne (120, 121, 122), of the "spermatogonia" and "spermatia" in both the lichens and the ascomycetes. His suggestion that these organs play some part in sexual reproduction, and might be the male reproductive organs, resulted in numerous investigations by de Bary (7), Cornu (21), Brefeld (13), and others of this question. These investigations have gradually discredited Tulasne's hypothesis, but it still persists in the back-ground of the biology of these fungi. A second important result of this part of Tulasne's work was the establishment of the pleomorphism of the ascomycetes, that is, the occurrence of two or more spore forms in the life history of one and the same fungus. In the three volumes of the "Selecta Fungorum Carpologia" of L. R. and C. Tulasne (123), are to be found excellent plates and numerous descriptions of their ideas of certain life-history connections of the conidial and perithecial stages of these fungi. Although based on observation and inference only, most of these life-history connections remain the most authentic we have for the species concerned.

In 1867, Füsting (36) published the first studies upon the developmental morphology of the stromatic Sphaeriales. He studied the develop-

ment of the stroma and perithecium in a number of species, and found coils of large, deeply staining hyphae, which he termed "Woronin hyphae," and which occurred in the perithecial initials of *Diatrype* (*Diatrypella*) *quercina*, *Eutypa*, and other forms.

In the latter half of the nineteenth century, there appeared a number of works on the taxonomy of the Pyrenomycetes; these systems were based on the accumulation of knowledge of the morphology and life histories of these forms since the time of Persoon and Fries. The systems of Nitschke (83), Fuckel (35), and Winter (132) in Europe, and of Ellis (29) in America, were based chiefly on the position, structure, and arrangement of the perithecium and stroma; these characters were used to distinguish the families of the Sphaeriales, while spore characters were generally used for generic separations. Saccardo (100), on the other hand, used spore characters for the separation of very large groups. These systems still remain as the principal classifications of the Sphaeriales.

In 1891, Brefeld (14, 15) published the results of extensive cultures of the stromatic Sphaeriales and of the ascomycetes in general. In 1900, Ruhland (99) undertook a study of the development of the stromatic forms of the Sphaeriales, and attempted to erect a phylogenetic scheme upon the basis of the development of the stroma.

From 1900 to the present time there have been numerous cultural studies of the life histories of various species of ascomycetes. Very few of these studies, however, have been of the stromatic forms. Most of the work has been upon more or less parasitic forms of economic importance. The work of Klebahn (67, 69, 72), Potebnia (95, 96, 97), Stone (113, 114, 115), Laibach (73, 74), Miles (81), and others on *Mycosphaerella*, *Gnomonia*, and other genera; of Miss Stoneman (116), Shear (107, 111), and Edgerton (26, 27) on *Glomerella*; of Harter (44, 45, 46) and Miss Jenkins (65) on *Diaporthe*; and of Wollenweber (134) on the perfect stage of *Fusarium* may be cited as examples of this type of work.

During this same period a second group of workers appeared in Europe, whose attention was focused on the morphology and taxonomy of fungi in general, and of the ascomycetes (including their imperfect stage) in particular. Chief among these were von Höhnelt, H. and P. Sydow, Theissen, Petrak, Rehm, and others. These workers were in touch with the large herbaria of Europe, and were able to study enormous numbers of specimens and to compare them with authentic type material of earlier workers. As a result of their work there is available a vast amount of technical data concerning the synonymy and detailed morphology of these fungi. The important result of the sifting of these data has been the recognition of certain broad relationships within the Pyrenomycetes.

The work of these men brings us to the present time. The systems of the earlier workers, since they were based upon a comparatively incomplete knowledge of the forms in question, was necessarily artificial and temporary.

The great mass of work on the Sphaeriales since that time has been in the shape of scattered and uncorrelated descriptions of species and genera. There has arisen, however, a large amount of information on both the cultural and the morphological sides, and it seems to the writer that the time is ripe for a new attempt to recast our knowledge of these forms along the lines of their natural relationships.

MORPHOLOGY AND TERMINOLOGY

Before entering upon a discussion of phylogeny it is necessary to understand the organisms that one is to consider. One needs at the outset, therefore, a clear idea of the structural morphology, biological characteristics, and terminology of the groups involved. Perhaps the most important point to be understood, before entering upon a discussion of the stromatic Sphaeriales, or of the fungi in general for that matter, is the extreme plasticity of their morphological characters. In these stromatic forms, the fruit bodies are surrounded by more or less differentiated vegetative hyphae. Slight variations in the character of the substratum, or in the factors affecting growth, cause variations in the type or amount of this mycelium produced. Such differences in growth often result in wide variations in the morphological characters of any species. In contrast to this rather wide individual variation, we find that the range of variation of the entire group is comparatively restricted in respect to just those characters which are widely variable in the species. These facts, together with that of the large number of species, mean that there are numerous intergrading and overlapping forms. Such a situation necessitates the consideration of very minute differences. There has been an all-too-great tendency, however, to separate species and genera without a sufficient conception of what the variation within a given species or genus might be under different conditions. Probably the best morphological example of this variation within a species is that of the stroma. It is the stroma which is supposed to be characteristic of the group here to be considered; and its variable structure is responsible for the numerous transitional forms occurring between so-called species.

Before going further, let us determine what the term *stroma* signifies. The term has had a widely varying usage. An examination of Orton's paper (86), which gives the history of this usage, will show the broad application of the term by various writers in the past. In examining this usage we find that the term *stroma* has been used most generally in the ascomycetes, and has been applied generally to the vegetative matrix of a fruiting structure. Such matrices are merely aggregations of vegetative mycelium and differ from the ordinary mycelium only in the compacting or coalescence of the hyphae. Sclerotia, and other sterile masses or bodies, *not associated with spore-bearing structures*, are identical in their histological nature with the matrices of various compound fruit bodies, and should be included in any definition of a stroma. Finally, as pointed out by Orton,

the tissues arising as a result of a sexual stimulus should be excluded from the conception of this term.

Ruhland (99) defines *stroma* (as distinguished from *mycelium*) as "die Gesamtheit derjenigen vegetativen [in contrast to the fruiting mycelium of the perithecium and the conidial hymenium] Bestandtheile des Pilzkörpers, welche ohne ausschliesslich der Resorption zu dienen, sich in irgend welcher Weise am Aufbau des Fruchtkörpers betheiligen." This definition, however, limits the term *stroma* to components of a compound fruiting body (see definition, p. 17), and does not sharply distinguish those tissues of a sexual fruit body which arise as a result of a sexual stimulus.

With these points in mind, let us define a stroma as an aggregation of vegetative mycelium not resulting from a sexual stimulus.

This definition is admittedly very broad. Numerous other terms have arisen, however, to designate the various types of stromatic structures and aggregations of mycelium, and it is considered that the term *stroma* should be used in this broad sense, to distinguish a type of mycelial differentiation rather than any particular morphological structure.² Such an aggregation of mycelium may be merely a loosely compacted mass; it may be a mixture of fungous hyphae and substratum tissue, or host tissue; or it may be a solid mass of fungous pseudoparenchyma or pseudoprosenchyma. Such a tissue may be symphogenous or meristogenous in origin. It may, or may not, have an outer differentiated crust. The type of cells, the darkened color of the cell walls, or its morphological structure does not alter its stromatic nature.

This definition, however, excludes tissues arising as the result of a sexual stimulus, such as the wall of the perithecium or the hypothecium of an apothecium. It also excludes such reproductive tissue as hymenial layers or other sporulating tissues, and does not include the purely nutritive mycelium of the vegetative portion of the plant.

Both Füsting (36) and Ruhland (99) have recognized the differentiation of the stroma of many twig-inhabiting fungi into two tissues, which they have designated as *epistroma* and *hypostroma*, and *ectostroma* and *entostroma*, respectively. The application of these terms by both writers clearly indicates differences in position and structure. These writers themselves, as well as others, have confused these terms, however, with *conidiostroma* and *ascostroma*, and have attempted to attribute to them a difference in function in their relation to spore-production. It is true that conidia are usually produced from ectostromatic tissue, and that perithecia ordinarily arise in the entostroma. In the majority of perithecial stromata, however, the ectostroma remains sterile and serves merely the mechanical function of rupturing the periderm. Furthermore, in many cases, as in

² This definition is applicable chiefly to the ascomycetes. The term is of such restricted usage in the basidiomycetes and other fungi that no attempt will be made here to discuss its meaning in those groups.

Eutypella or the subgenus Leucostoma, the conidial locules ordinarily arise within the entostromatic tissue. These terms will be limited, therefore, to designate differences in structure and position, and not in function. They may be defined as follows:

An *ectostroma*, in the Pyrenomycetes, is that portion of the stroma which is formed on the surface of the bark, beneath or within the periderm, and which consists typically of fungous tissue only, except that when it is developed within the periderm it may contain the remnants of the periderm cells, but never of the bark cortex cells.

An *entostroma*, in the Pyrenomycetes, is that portion of the stroma which develops within the cortical or woody tissue of the host or substratum and is made up of components of both fungous and host tissue or substratum tissue.

These terms were coined for tissues produced in a group with a special type of development, and can not be applied to all fungi, any more than the term *perithecium* can be applied to the Discomycetes.

The ectostromatic and entostromatic tissues, in some species, as in *Diatrype stigma*, are sharply differentiated. It must be remembered, however, that the ectostroma arises from the same mycelium within the bark tissues which proliferates to form the entostroma, and therefore in many cases, as in certain species of *Diaporthe*, the distinction between these two tissues is not sharply defined. In other cases, as in the genus *Valsaria*, the entostromatic mycelium becomes so strongly developed that it forms an erumpent stroma composed largely of fungous tissue, which may superficially resemble an ectostromatic structure. Wherever we attempt to apply sharply defined terms to living organisms this same situation will be met. There will always be variations which can not be rigidly interpreted. Neither does a multiplication of terms help this situation. The use of qualifying statements is necessary for these intergrading forms.

Let us now turn to the origin and development of the stroma in the Sphaeriales, in order to trace its variation in the different groups. The stromatic Sphaeriales have apparently arisen from the simpler forms of the Pyrenomycetes by acquiring the habit of forming their perithecia immersed in the host or substratum tissue. This habit, in turn, could not be acquired until the mycelium had become capable of penetrating this tissue. Just as all fungous structures are made up of mycelial elements, so, likewise, has the stroma arisen through a development and differentiation of the immersed mycelium. The first evidence of a primitive stroma appears as a blackening of the surface of the substratum. Such a condition may be seen in many species of *Eutypa* and of the subgenus *Euporthe*. The next step in stromatic development comes about by the proliferation of the mycelium within the substratum. As this formation of mycelium increases, it usually becomes more or less localized about the forming perithecia. With this differentiation of an entostroma, there is usually correlated, very

often beneath a differentiated ectostroma, a clustering of the perithecia. This mode of organization of a compound fruiting structure is in reality the formation of a stroma immersed within the bark tissue. Just as most superficial stromata form an outer layer of darkened thick-walled cells upon contact with the air, so does this immersed stroma form a zone of similar blackened tissue about its margin. This is the blackened zone outlining the stromatic areas, which is so common in the stromatic Sphaeriales. This marginal zone of blackened tissue protects the stromatic areas from the absorptive action of the nutritive hyphae in the adjoining bark tissues, as has been shown by the writer for *Cryptosphaeria populina* (Pers.) Sacc. (129). The entostromatic hyphae themselves, which bind together the bark cells of this area, act as a protective and nutritive tissue for the developing perithecia.

As one passes from the most primitive to the most highly developed stromatic forms, these various stromatic characters show all degrees of variation in the different species. These variations in stromatic configuration have been largely used as characters for the separation of various groups. Ruhland (99) attempted to work out the phylogeny of this group on the basis of the stromatic development. His reasoning was based chiefly on the type of tissue concerned in, and the manner of, the bursting of the periderm. These are valuable diagnostic characters, but, in the writer's opinion, Ruhland's attempt has failed for two fundamental reasons. In the first place the phylogeny of no group can be determined from one set of characters alone, without the consideration of the development and correlation of other characters. Secondly, the stroma of the Sphaeriales has arisen and developed independently in several separate groups, in a more or less nearly parallel manner.

A number of terms have been used to describe the various types of stroma. Any particular stromatic configuration, however, is made up of a number of characters which vary independently. As a result we may have any combination of, or variation between, these characters. In a discussion of relationships it is more clear, therefore, to speak of the stroma in terms of these varying characters than to speak of fixed types of stromata (as Valsoid or Eutypoid) which designate combinations of such characters fitting only special cases. It is hoped, therefore, that the following account of the terms to be used for these characters will aid in a clear understanding of what follows.

The term *compound fruit body* will be here used to designate the type of fruiting structure which consists of an aggregation of a number of perithecia seated upon, included within, or oriented beneath, a stromatic tissue. In its highest development, in the forms here discussed, such a compound fruit body consists of a number of perithecia included within a differentiated entostromatic tissue and oriented beneath an erumpent ectostroma. This type of fruit body has developed from scattered simple perithecia, and as a

result all intermediate variations are to be found. This term must, therefore, designate a type of structure towards which the course of development tends, rather than any sharply definite type of organization.

A *fruiting area* will be considered as including the entire area of the substratum in which perithecia or compound fruit bodies are produced.

The perithecia within a fruiting area may be scattered or clustered. There are varying degrees of the grouping of the perithecia, but these can be indicated.

There may, or may not, be a development of entostromatic mycelium about the scattered or clustered perithecia, within a fruiting area.

If an entostromatic mycelium is developed about the perithecia, such an entostromatic area may or may not be surrounded by a darkened marginal zone.

The entostromatic area is often lighter in color than the surrounding bark tissue, on account of the development of a hyaline mycelium within this area, or the darkening of the disintegrated bark tissues outside this area, or both. Such an area will be designated as a *differentiated entostromatic area*.

The ostioles of the perithecia within a fruiting area may be *separately erumpent* or *collectively erumpent*. Clustered perithecia, or the perithecia within an isolated stroma, as in *Diatrype*, may have separately erumpent ostioles.

An entostromatic area (stroma) will be spoken of as *effused* when it contains numerous separately erumpent perithecia, or more than one cluster of perithecia either separately or collectively erumpent; and as *isolated* when it contains only one cluster of perithecia, either collectively or separately erumpent. The differentiation between isolated and effused stromata, in such cases as the genus *Diatrype*, must remain purely arbitrary, as it depends merely upon the areal expansion of the stroma.

The *disc* (*Placodium* of Ruhland) is that portion of the stroma which is erumpent through the periderm or epidermis. Such a disc is not always present, for in some species the perithecial neck may burst through the periderm by means of the mechanical pressure of its own growth, or may grow upwards as a mass of hyphae which push their way through the periderm by means of their disintegrating action. This disc may be composed of ectostromatic tissue (*ectoplacodialer* type of Ruhland, as in *Diaporthe*), or of entostromatic tissue (*entoplacodialer* type of Ruhland, as in *Diatrype*). When the disc is ectostromatic, it may consist of a sharply differentiated conical stroma, or it may be an irregular pulvinate mass, so intimately intergrown with a well developed entostroma within the surface bark layers that no sharp distinction can be drawn between the two tissues.

The ostioles, which are merely the erumpent portion of the perithecial necks (*Tubulus* of Füssing), may vary greatly in length in certain species, depending upon the moisture conditions. The tips of the ostioles may be

punctate, that is, merely perforated by the circular opening of the central canal; or they may be *sulcate*, that is, have 3-5 clefts or grooves in the apex of the wall of the central canal.

The size and shape of the perithecium is of diagnostic value only in the occasional separation of species. The perithecia may be arranged parallel to one another and perpendicular to the surface; they may converge towards, or be arranged *circinately* (in a circle) about, a central disc; they may be *monostichous* (in a single layer), or *polystichous* (in two or more irregular layers); or they may be imbedded in a variously developed stroma, or in the unaltered bark cortex.

The work of recent European mycologists, von Höhnelt in particular, has brought out the importance of what they have termed the perithecial "Nukleus," in determining broad general relationships. This term is used to include the totality of structures within the perithecial wall. The application of the term *Nukleus* to this aggregate of structures is ambiguous and very misleading. In the following discussion the term *perithecial centrum* will be used instead. This perithecial centrum includes the asci, paraphyses, and the inner portion of the perithecial wall (subhymenium).

The spores themselves provide one of the most nearly constant and dependable characters that we have. Objections have been raised to the over-emphasis upon spore characters. The consideration of spore characters alone of course gives rise to the same sort of errors to which the exclusive use of any one character leads. Similar spore forms have arisen in different lines of evolution, and correlated characters must be used to determine their true relationships. Some species are slow in attaining the final coloration or septation of their spores. Certain species of *Pseudovalsa*, for instance, do not show the coloration of their spores until they are fully mature. The consideration of immature spores of such species has also led to confusion. The variations in any given species can be determined more easily, however, in the case of spore characters than in that of almost any other character, since the variations are usually characteristic for a species and not due to environmental conditions. The spores may be uniseriate or biseriate in the ascus, may possess various types of appendages or gelatinous envelopes, may be hyaline or colored, variously septate, and of various shapes. Spore size is valuable chiefly as a specific character.

The structure of the asci and their arrangement in the hymenial layer have been shown by von Höhnelt to be important characters in the separation of large related groups. The asci may be 4-, 8-, or many-spored. They may have more or less elongated persistent stalks and form a definite hymenial layer; or their stalks may be delicate and evanescent, and the asci may lie irregularly massed in the perithecium. The asci may be clavate to cylindrical, with variously thickened tips or pores.

The presence or absence of paraphyses has been much used in the separation of species, genera, and even families. Wherever this character has

been used as a major character, confusion has arisen. It is rather the rule than the exception to encounter contrary statements by different authors as to presence or absence of paraphyses in any given species. The paraphysis-like structures in the Sphaeriales are of the "pseudo-paraphysis" or "metaphysis" type of Petrak (92, pp. 65, 68). A consideration of the character and development of these structures easily explains the situation. They arise as numerous delicate, filiform hyphae; they appear before the asci, and apparently act as a nurse tissue to the developing asci. In many species they are entirely used up, or absorbed, by the growth of the asci; in other species delicate remnants persist in the mature perithecium; while in still other forms these paraphyses are more numerous and persistent, and appear in large numbers in the mature perithecium. There is a gradual increase in the number and persistence of the paraphyses as one passes from the simpler to the higher forms, in certain developmental series. There are two facts, however, which make the use of these structures as diagnostic characters unreliable. In the first place, their number and visibility vary with the degree of maturity of the perithecium. Secondly, the paraphyses, when only sparsely present, are, on account of their delicacy and transparency, difficult to distinguish even under the best microscopic definition. As a taxonomic character, therefore, they should be used only in correlation with other characters.

TAXONOMY

The taxonomy of the ascomycetes is at present one of confusion. On account of our inadequate knowledge of the life-history connections of the spore forms of these fungi, the separate classification of the imperfect spore forms, as form genera, will probably always remain as the only convenient and practical means of their identification. The chaotic condition of the classification of the fungi imperfecti need not be discussed here; it is self-evident.

The taxonomic literature of the Sphaeriales is riddled with inaccuracy and confusion. It is this chaotic condition of the synonymy which has apparently discouraged any comparative study of the group. The old systems of Fuckel and Nitschke still stand with very few improvements. One need make only a superficial examination of the pages of Saccardo's "Sylloge" to be impressed by the numerous inadequate and even inaccurate descriptions of species and genera. Any herbarium will show inaccurately determined exsiccati and immature or half-decayed material; and many a species has been described from such an impossible remnant. The scattered condition of the literature containing specific descriptions should discourage the description of new species, but the result is apparently the opposite, judging from the multiplication of species and the resulting duplication. It is apparently easier to describe a specimen as a new species than to identify it. Until the recent publications of von Höhnelt, Sydow, Theissen, Petrak, and other European mycologists, no comparative study, or effort to sift or

arrange this mass of scattered and often worthless material and data, had been undertaken. These workers have straightened out much of the synonymy and morphology of numerous European species, and have pointed out many of the broader relationships.

This later work, however, has emphasized minute structural differences without a proper appreciation of the variation of such structures within a given species. The generic concept has likewise become narrowed. There seems to be a general practice at present to erect new genera for every slight variation from the type species. This method employed by a number of separate workers, with various viewpoints, leads to a large number of monotypic genera. This tendency is apparently due to two causes. In the first place, the limits of the old genera are indistinct; in the second place, we have no fixed ideas as to the relationships within the larger groups. Most of the characters of the sphaeriaceous fungi seem to vary independently of one another, and the tendency to erect a new genus for each different grouping of characters will result in an enormous number of artificial genera, each containing one or a few species. On the other hand, genera separated on the basis of the correlated characters of a developmental series must necessarily have arbitrarily chosen limits. This is true because of the numerous transitional species in any developmental series. The position of such transitional species, however, is always definitely fixed in the phylogenetic scheme, no matter what arbitrary generic lines are chosen. Whatever method of separation is used, however, genera should not be erected in a haphazard manner upon one or a few species without a thorough knowledge of the relationships and variations of the other species of the group in which the genus lies. The present confusion of newly erected, recently abandoned, vaguely distinct, and often overlapping genera speaks eloquently against such a practice.

The first step, as the writer sees it, is to attack each large natural group as a whole. Luckily the preliminary step of collecting, collating, and assimilating a large amount of data has to a large extent been done by the European workers just mentioned.

The imperfect stage has long been used to obtain evidence for relationships in the Sphaeriales. Nitschke and Winter have used the type of conidial fruit body as a character in the separation of the Melanconideae and Melogrammaceae. The genera *Scoptria*, *Melanconis*, and many others have been separated more or less upon the basis of the imperfect stage. Recently Klebahn (72) and Wollenweber (134) have used the imperfect stage as a means of separating genera. Von Höhnelt and Petrak have also used this method in erecting new genera. The conclusions of these two workers have been drawn, however, from observational associations in a comparatively small number of species, rather than from cultural connections of a large number of related forms. With the increasing tendency to consider the entire life history of these fungi in determining their classifica-

tion, it becomes more and more essential to have a number of authentic connections of perfect and imperfect stages, in order to determine the relationships of species and genera.

On account of these facts, and because the writer considers that a study of the complete life histories and morphological development of a large number of forms is necessary to an understanding of the phylogeny of any group, single-spore or single-ascus isolations have been made of a large number of species of the group under consideration, and their life histories have been worked out in culture. Detailed accounts of most of these studies have been published in separate papers (127, 128, 129, 130), or are now in press. The following forms have been studied in culture.

SPECIES CULTIVATED

Life histories published:

1. *Diaporthe oncostoma* (Duby) Fck.
2. *Quaternaria Persoonii* Tul.
3. *Diatrype virescens* (Schw.) E. & E.
4. *Diatrypella Frostii* Pk.
5. *Valsaria exasperans* (Ger.) E. & E.
6. *Valsaria insitiva* Ces. & de Not.
7. *Diaporthe furfuracea* (Fr.) Sacc.
8. *Diaporthe albovelata* (B. & C.) Sacc.
9. *Valsa Kunzei* Fr.
10. *Diaporthe binoculara* (Ell.) Sacc.

Life histories in press:

11. *Diatrype stigma* (Hoffm.) de Not.
12. *Cryptosphaeria populina* (Pers.) Sacc.
13. *Cryptosphaeria eunomia* (Fr.) Grev.
14. *Eutypella cerviculata* (Fr.) Sacc.
15. *Diaporthe galericulata* (Tul.) Sacc.
16. *Diaporthe obscura* (Pk.) Sacc.
17. *Eutypella tumida* (E. & E.) comb. nov.
18. *Eutypella fraxinicola* (Cke. & Pk.) Sacc.
19. *Cryptovalsa Nitschkei* Fck.
20. *Cryptovalsa* sp.
21. *Diatrypella quercina* (Pers.) Nit. f. *crataegi* E. & E.
22. *Diatrypella favacea* (Fr.) Nit.

Life histories not yet published:

23. *Diaporthe marginalis* Pk.
24. *Pseudovalsa longipes* (Tul.) Sacc.
25. *Diaporthe faginea* (Curr.) Sacc.
26. *Diaporthe pruni* E. & E.
27. *Diaporthe* sp.
28. *Cryptospora cinctula* (Cke. & Pk.) Sacc.
29. *Cryptospora* sp.

THE PHYLOGENY OF THE STROMATIC SPHAERIALES

It is the intention of the following discussion, then, to consider in some detail the relationships that may be made evident by a consideration of the stromatic forms of the Sphaeriales, chiefly of the families Valsaceae, Melanconidaceae, Melogrammataceae, and Diatrypaceae, from the various viewpoints just discussed.

In the discussion of the imperfect stages, stress will be laid on the morphological and developmental similarities. As the nomenclature of this group is confused and misleading, the position and synonymy of these forms will be considered only in a general way.

The four families of the Sphaeriales just mentioned fall naturally into two large classes, each of which is characterized by a number of correlated characters. Von Höhnelt (59, 60) recognized the existence of these two large groups of forms in the Sphaeriales, and designated them as the "Allantosphaeriaceen" and the "Diaporthen." He based his separation of these two families upon the internal structure of the perithecium, which he termed the perithecial "Nukleus" and which is here spoken of as the perithecial centrum. We shall see as we proceed with the discussion of these two groups that there are other characters, in both the perfect and the imperfect stages of the life histories of these fungi, which are correlated with this difference in the perithecial centrum.

Allantosphaeriaceae

In his family of the "Allantosphaeriaceen," von Höhnelt (56, p. 54; 60, p. 127) included four subfamilies, which he named the Diatrypeen v. H. (non Aut.), Calosphaeriaceen v. H., Valseen v. H., and Coronophoreen v. H. His Diatrypaceae and Valsaceae are the two families of particular interest in this discussion. The Calosphaeriaceae and Coronophoraceae are chiefly non-stromatic forms, and have not been studied by the writer. The Valsaceae, although resembling the Diatrypaceae in the allantoid character of their spores, differ in almost every other point and in reality belong with the Diaporthaceae. Von Höhnelt himself recognized this fact, for he said: "Die Valseen sind allantoidsporigen Diaporthen und werden daher in dem endgültigen System der Sphaeriaceen zu denselben gebracht werden müssen, da mir der Bau des Nukleus wichtiger erscheint als die Sporenform" (60, p. 129). Our discussion here, therefore, narrows down to his Diatrypaceae, which contain, besides the old genera *Diatrype*, *Quaternaria*, and *Diatrypella*, all the subgenera of the genus *Valsa* Nit. except *Euvalsa* and *Leucostoma*. The genus *Endoxyla* also belongs in this group. In his discussion of the "allantoidsporigen Sphaeriaceen" (60), von Höhnelt excluded *Endoxyla*, having previously placed it with the genus *Anthostoma* (53). In a later paper (63), however, he recognized *Endoxyla* as an allantoid-spored form. The genera *Anthostoma* and *Valsaria*, although not having allantoid spores, show many other characters of this group, and will be discussed under this heading in this paper.

The first striking resemblance common to the members of this group is the structure of the perithecial centrum, which was thoroughly investigated and recognized by von Höhnelt. All these forms, except the genera *Valsaria* and *Anthostoma*, have allantoid spores (in *Anthostoma*, the spores are inequilateral or slightly curved, and in some species of *Valsaria* they are curved). The spores are also always more or less colored, ranging from a dilute yellowish hyaline in some species of *Eutypa* to a dark brown in *Anthostoma*. They are usually one-celled, but become septate in a few genera, as in *Endoxyla*. The spores are biseriate in the ascus (becoming obliquely uniseriate, or uniseriate in *Anthostoma* and *Valsaria*). In contrast, the genera *Euvalsa* and *Leucostoma* have purely hyaline spores. The structure and arrangement of the asci is also characteristic in the *Allantosphaeriaceae*. The asci are 8- or many-spored, clavate, often with a thickened tip in some genera, always more or less equally long-stipitate, and arranged in a definite hymenial layer covering the base and sides of the perithecium. This occurrence of more or less persistent ascus stalks of equal length gives rise to the regular more or less colored layer of spore-bearing asci about the margin of the perithecial cavity, so characteristic of this group. Paraphyses are typically present, becoming gelatinous in age. The ostioles of the group are characteristically sulcate. The evolution of the stroma in this group shows that the entostroma has first arisen as a broadly effused tissue and has later become limited in area, resulting in isolated stromatic patches. Each of the series to be discussed shows transitional variations from the effused to the isolated type of stroma. The stroma, therefore, can not be used to separate genera but is of value in tracing the development within a series, when used in connection with other correlated characters. *Hypoxylon*, *Diatrype*, *Anthostoma*, and *Diaporthe* in the traditional sense, for instance, all include both effused and isolated types of stromata in various species.

Another very constant character in this group is the imperfect stage. The conidia, called spermatia by the earlier writers, are always more or less elongated-cylindrical to filiform, hyaline, one-celled, and more or less bent or hamate. These conidia are formed in enclosed locules or in more or less exposed layers, either in ectostromata on the bark surface or in the entostroma within the bark cortex. Some of the more primitive effused forms also produce conidia on free conidiophores. These variations in the configuration of the hymenium and stroma may be found within the same species (especially in culture), as well as between species.

From the preceding discussion we see that von Höhnelt's "*Allantosphaeriaceen*," including the genus *Endoxyla*, but exclusive of his "*Valseen*," form a compact and related group of species, with a number of correlated characters in common. It is reasonable to assume that a number of species showing so many characters in common, in both stages of their life history, form a phylogenetically related group. Such an assumption is strengthened

by the fact that there can be traced within this group four parallel series of species, which arise from the more primitive forms and show the gradual evolution of the stroma and the isolated compound fruit body. These series differ from one another in the type of stromatic development, as well as in certain correlated morphological characters.

Let us now turn to a consideration of the relationships within these series.

Eutypa and Cryptosphaeria

Since the origin of the stromatic Sphaeriales from the simple Sphaeriales is characterized by the development of a stromatic tissue in connection with the perithecial fruit bodies, it is natural to suppose that this character will be the one which will be the most plastic and will show the greatest variation. One would not expect the development of such a character, due probably to a change in life habit such as the formation of immersed perithecia, to be a monophyletic one. It would be more logical to suppose that such a development began in a number of separate species with immersed perithecia, belonging to widely separated genera. The existence of a stromatic tissue about the fruit bodies of species with widely varying spore and perithecial characters supports this view.

Assuming such a polyphyletic origin, we should expect that the main lines of stromatic development in any large group, such as the Allantosphaeriaceae, would arise from a group of species with a primitive type of stromatic development but a comparatively wide range of variation in other associated characters. This is precisely the case. The effused stroma, or protostromatic type of Ruhland, is usually considered as the more primitive form and most closely related to the simple Sphaeriales. This by no means should imply, however, that all effused stromata are of a primitive type. The effused Diatrypes and Hypoxylons, for instance, show an advanced type of stromatic development. The taxonomy of the effused forms is in a confused condition. The genera *Eutypa*, *Cryptosphaeria*, *Cryptovalsa*, *Diatrype*, *Endoxyla*, and *Anthostoma* all contain effused forms. This means in other words that all these genera can be derived from forms with a primitive type of stroma.

The species of the genera *Eutypa* and *Cryptosphaeria*, here to be considered, are probably the most primitive of these species with an effused stroma.

Greville's (39, no. 201) conception of the genus *Cryptosphaeria* was very broad, including even pycnidial forms which are immersed in the substratum. The subsequent descriptions of the genus have been exceedingly brief, and in no way delimit it from the Tulasnes' (123, p. 52) description of the genus *Eutypa*. The only existing difference seems to be that all species of *Cryptosphaeria* are immersed in the bark, while most of the species of *Eutypa* inhabit decorticated wood. Many species of *Eutypa*, however, are described which inhabit the bark cortex, and many of these

species can undoubtedly exist in either condition. As the species of these two genera are also often confused with the lower forms of the genera *Diatrype* and *Eutypella*, it will be necessary here to disregard more or less the present taxonomic position of these species and to seek for relationships instead.

In our later discussions of the *Allantosphaeriaceae*, we shall have occasion to differentiate between those species which do, and those which do not, form conidial locules in the entostromatic tissue of the bark. Although too little is known as yet of the species of these two genera to make any sharp differentiation in this respect, yet there seem to be certain groups of forms which may serve as possible examples of the origin of these conditions.

The most primitive types of the genus *Eutypa* are probably represented by such forms as *Eutypa Acharii* Tul., *E. lata* (Pers.) Tul., and *E. spinosa* (Pers.) Tul., which grow on decorticated wood. These forms seem to represent the origin of the types with an ectostromatic conidial fruit body. The perithecia of these species are rather evenly scattered just within the wood. There is a very sparse development of entostromatic mycelium, but pockets, or scattered hyphae, of a black-walled mycelium are often found within the wood. As a result, these stromata are not raised above the surface of the substratum. The surface of the substratum is more or less blackened by the growth within the surface layers of the wood tissue of dark-walled hyphae, which blacken and disintegrate the cells and form a blackened crust. This blackening is the only evidence of a stroma. These dark-colored hyphae may give rise to a hyphomycetous conidial stage, consisting of free, septate, brown conidiophores bearing hyaline curved conidia. This formation of brownish hyphae in the surface layers of the substratum, and the occurrence of a hyphomycetous stage, are characteristic of many simple *Sphaeriales*, certain superficial wood-inhabiting forms in particular.

Other species of this primitive type, as some specimens of *Eutypa lata* (Syd. Myc. Germ. no. 234), show a richer development of mycelium within the wood, as a result of which the stromatic areas become somewhat raised above the general surface of the substratum. This indicates the beginning of entostromatic development. The surface of the stroma is, however, always covered by a blackened crust of the substratum.

Two types of imperfect stages have been described for the species of *Eutypa* just discussed. The first of these consists of a hyphomycetous stage of free, septate, brown conidiophores, bearing clusters of filiform, curved, hyaline, one-celled conidia. This hyphomycetous stage, as already mentioned, shows the close relationship between these species and the simple *Sphaeriales*. Such free conidiophores have been figured by the Tulasnes (123, Pl. VII, figs. 9, 10) for *E. Acharii*, and have been described by Füsting (36, p. 193) for *E. lata*. Brefeld (14, pp. 238, 239) grew several species of *Eutypa*, and obtained a free conidiophore stage of *E. sublecta* Fr. but failed to obtain this stage of *E. Acharii* in culture.

The second type of imperfect stage in these species consists of a conidial hymenium formed in or on an ectostromatic cushion. These hymenial layers may be in enclosed locules, open cavities, or exposed layers, but are always formed in or on a stromatic cushion arising on the surface of the entostroma. The Tulasnes (123, Pl. VII, figs. 8, 9, 11) figure such a conidial stage for *E. Acharii*, and Füsting (36, p. 193) describes similar ones for *E. Acharii* and *E. lata*. Brefeld (14, p. 239) obtained such conidial stromata in cultures of *E. Acharii*.

This formation of the conidial hymenium in ectostromatic cushions is most important, for it is the development of this ectostromatic tissue which characterizes the *Diatrype* series, as will be seen later. Füsting (36, p. 193) states that ectostromata are formed by *E. lata* and *E. flavovirescens* only when they grow on bark, and that, when growing on decorticated wood, *E. lata* seldom develops sufficient ectostromatic tissue to produce conidial tissue. This would support the view, which the writer here puts forward, that the development of the ectostroma has resulted from the formation of the perithecia within the bark, and from the concomitant necessity of producing some sort of mechanical tissue for the rupture of the periderm.

The second type of *Eutypa*-like forms to which the writer wishes to call attention includes the species of *Cryptosphaeria* and such forms as *E. flavovirescens* (Hoffm.) Sacc., and *Diatrype Hochelagae* E. & E. The chief differences between these forms and those previously mentioned are the greater development of the entostromatic tissue and the formation of the conidial locules within this tissue.

Eutypa flavovirescens (Hoffm.) Sacc. shows a rather special development and possesses characters which suggest its intermediacy between the two groups of species here considered. It may be found growing either on decorticated wood or in bark. The stromatic tissue, which is developed beneath the surface layers of the substratum cells, is very strongly developed and yellow-green in color. The perithecia are formed in this tissue, which is composed almost entirely of fungous hyphae and forms a raised stromatic area. On wood it is covered by several layers of the wood cells, but on bark it bursts open the periderm. The conidial locules of this species are formed within the entostromatic tissue, within which the perithecia arise. The Tulasnes (123, Pl. VII, figs. 3, 4) figure this imperfect stage, and it has been described by Füsting (36, p. 193). Brefeld (14, p. 239) grew *E. flavovirescens* and obtained free conidiophores which often united to form *Coremia*-like structures. The formation of free conidiophores shows that this species, in spite of its well developed entostroma, is closely related to the more primitive forms of the preceding group.

Diatrype Hochelagae E. & E., which is not a *Diatrype* but a *Eutypa*, has a structure very similar to *E. flavovirescens*, with the exception that the entostromatic mycelium is hyaline instead of yellow-green. It occurs on decorticated twigs of *Ulmus*, and is very similar in structure to *Diatrype*

(*Eutypella*) *tumida* E. & E., found on bark of the same host. It therefore represents a type from which the species of *Eutypella* have probably arisen.

The species of *Cryptosphaeria* show a more advanced type of stromatic structure than the species already mentioned. *Cryptosphaeria populina* (Pers.) Sacc. may be taken as an example of this genus. The writer has carried this species in culture, and a more complete account of its development may be found in a previous paper (129). This species grows in the bark of various species of *Populus* and forms a distinctly differentiated entostromatic area, outlined by a zone of blackened tissue. There is formed, on the surface of the bark beneath the periderm, a layer of closely interwoven and heavily blackened hyphae. This might be considered ectostromatic tissue, but is more likely homologous to the blackened hyphae in the surface layers of the substratum of such species as *E. Acharii*, etc., since it does not function as either a mechanical or a spore-bearing tissue. The important points to keep in mind in connection with this species are the lack of any hyaline ectostromatic tissue, the entire lack of any rupturing of the periderm, the separate emergence of the perithecial necks through the periderm, and the presence of numerous filiform paraphyses in the perithecium. These characters, we shall later see, suggest this species as a type giving rise to the fourth and last series of the *Allantosphaeriaceae*.

The imperfect stage of this species was not obtained in either agar or twig cultures.³ Saccardo (100, vol. 3, p. 602) gives *Cytosporina myriocarpa* Sacc. as the imperfect stage of *Cryptosphaeria myriocarpa* (Wint.) Sacc. This *Cytosporina* is described as forming chambered locules beneath the periderm in the entostroma. This entostromatic origin of the conidial locules is probably characteristic of the genus *Cryptosphaeria*. All the conidia of this second group of *Eutypa*-like forms, so far as they are known, are of the typical filiform, hyaline, curved character.

It is such forms as those just named which represent the logical origin of those two series of the *Allantosphaeriaceae* that show the formation of the conidial locules in the entostromatic tissue of the bark. Correlated with this character is the lesser development of ectostromatic tissue in these series.

The two groups of species in question are taken as examples of a large number of forms with a primitive type of stroma which show numerous variations. Our knowledge of these forms, and particularly of their development, is very incomplete, but they undoubtedly compose the group of species from which all the lines of development within the *Allantosphaeriaceae* diverge.

³ The imperfect stage of *Cryptosphaeria populina* has recently been obtained in culture by the writer on twigs of *Populus grandidentata* Michx. which had been coated with paraffin. The conidia formed were filiform, hyaline, and curved, and measured $17-21 \times 1-2 \mu$. They were produced in ellipsoid locules within a stromatic tissue, which arose within and beneath the periderm. This stromatic formation was abnormal, for perithecia were produced in this same tissue. No definite conclusions can therefore be reached as to the ecto- or entostromatic nature of the normal pycnidia.

First Series: Diatrype

This first series includes the species of the genus *Diatrype* possessing either an effused or an isolated stroma. This series is characterized by the formation of a strongly developed deciduous ectostroma, which throws off the periderm from the entire surface of the equally well developed entostroma, whose darkened surface layers then form the widely erumpent disc. This strong development of the entostroma gives a characteristically distinct and abrupt margin to the strongly erumpent stroma. The perithecia are usually arranged parallel to one another in a single layer; they have short, stout necks and are separately erumpent through the encrusted surface of the entostroma as sulcate, disc-like ostioles. The conidia are always formed from ectostromatic tissue. The hymenial layers may be formed in enclosed locules, or in more or less open cavities. The conidia are long-filiform, one-celled, strongly curved, and hyaline.

We have seen that *Eutypa Acharii* possesses ectostromatic cushions in which such conidial cavities are formed, and it is from such primitive forms that the species of this series have probably arisen. At the present time there are no types of development known intermediate between that of *E. Acharii* and that of *Diatrype stigma*, which shows a rather advanced stromatic structure. If the development of some of the numerous transitional species of *Eutypa* were worked out, however, they would undoubtedly reveal such intermediate steps in the development of the stroma.

The Tulasnes (123, Pl. VI) described and figured *Diatrype stigma* under the name of *Stictospheria Hoffmanni* Tul. Füsting (36) studied the development of this species from field material. The writer has carried this species in pure culture and has published an account of its life history and development in a previous paper (129). The stroma of this species, although effused, shows an advanced type of development. The perithecia are imbedded in a strongly differentiated entostroma, bounded by a blackened marginal zone. There is early developed, on the bark surface, an effused layer of ectostroma which swells rapidly at maturity and throws off the periderm over large areas. This exposes the developing entostroma, whose surface then rapidly becomes blackened, forming the erumpent disc. The young ectostroma increases greatly in thickness at various points, and in these cushions of tissue labyrinthiform conidial locules are formed. Füsting (36) describes conidia of three sizes ($24-30 \times 0.5 \mu$, $10-18 (20-30) \times 1 \mu$, and $6 \times 1 \mu$). The Tulasnes (123, p. 50) mention only the small allantoid type, measuring $4-6 \times 1 \mu$. The writer found only one type of conidia in his cultures. These were crescent-shaped, hyaline, and measured $9-10 \times 1-1.5 \mu$. It is possible, of course, that there are several closely related species with different conidia.

The distinction between effused and isolated stromata in the genus *Diatrype* is purely an arbitrary one, based upon the areal expansion of the stroma. Some specimens of *D. stigma* itself show stromata of much more restricted extent than other specimens of the same species.

Diatrype bullata (Hoffm.) Fr. illustrates the further reduction of the area of the individual stroma. The stromata of this species are only slightly raised above the substratum, and are only 2-5 mm. in diameter.

The distinctly isolated type of stroma, as found in *Diatrype albopruinosa* (Schw.) Cke., *D. virescens* (Schw.) E. & E., *D. disciformis* (Hoffm.) Fr., *D. tremellephora* Ell., and many others, is usually 1-3 mm. in diameter. These isolated stromata have the same type of development as has *D. stigma*, except that it is confined to a smaller area.

In his discussion of the development of the stroma of *D. disciformis*, Ruhland (99) states that a strongly developed ectostroma is formed which is later thrown off by the development of the entostroma beneath. This same behavior is shown in a striking manner by Ellis' specimen of *D. tremellephora* (N. A. F. no. 775) on *Magnolia glauca*. The strongly developed ectostroma of this species breaks through the thick periderm and appears on the surface as a small reddish "tremelloid" disc, which swells greatly upon being moistened. This ectostroma is later thrown off by the entostroma, which then becomes the erumpent disc.

In these forms with an isolated stroma the entostroma is very strongly developed and is composed almost entirely of fungous hyphae. As a result the stroma is strongly erumpent and sharply defined. We shall see later that structures very similar to these *Diatrype* stromata have arisen in other evolutionary series. None of these, however, shows the deciduous ectostroma, and they are arrived at by a different type of development.

The imperfect stages of these isolated forms are also ectostromatic. The ectostroma above developing perithecia often remains sterile, but a conidial hymenium may be formed in open cavities upon the sides or flanks of such a conidial ectostroma. Such a conidial formation is described by Ruhland (99) for *D. disciformis*. Where ectostromatic growth is rapid and no perithecia arise beneath this tissue, labyrinthiform locules may be produced within these ectostromata. The upper portion of the stroma is often used up in conidium-formation, and the locules become exposed as open cavities. Brefeld (14) grew *D. disciformis* and *D. bullata* and obtained in both cases mycelial cushions, within which were formed irregularly enclosed conidial locules.

The writer has carried *Diatrype virescens* in pure culture and obtained various types of conidial fructifications. On agar these were irregular cavities formed within a superficial mycelial mass. On beech twigs under dry conditions they consisted of a basal stroma, often with a dome-shaped central portion. The surface of this stroma was covered with a conidial hymenium (127, Pl. XXII, fig. C, 5). Under moist conditions on beech twigs the ectostromatic cushion developed extensively and formed an erumpent superficial stroma, with a hymenium on its surface and within irregularly exposed cavities sunken in the stroma (127, Pl. XXII, fig. C, 6). This variability is characteristic of these ectostromatic conidial fruit bodies.

It can be seen from what has been said that the genus *Diatrype* in itself presents a distinct line of development from the effused to the isolated type of stroma. This phylogenetic series is different from all others of this family in the formation of a deciduous ectostroma, which exposes the darkened surface of the entostroma as a widely erumpent disc.

Quaternaria

This genus is rather ill defined, and some of its species undoubtedly belong to other genera. Two species have been studied by the writer. One of these, *Q. Morthieri* Fck., is, as Winter (132, p. 826) suggests, a species of *Anthostoma*. The second species, *Q. Persoonii* Tul., which is the type species and characteristic of the genus, has been carried in pure culture by the writer, and its life history has been published (127). This species does not belong in the same series as the genus *Diatrype*, but occupies an isolated position and shows a peculiar combination of characters representative of several of the series of the *Allantosphaeriaceae*. It is discussed here on account of the ectostromatic character of its conidial stage.

The perithecia of this species are in small groups of 2-4 within the upper bark tissues. The lower bark tissues and wood surface are blackened. There is a development of entostromatic mycelium about the perithecial groups, giving them a pustulate appearance. This mycelium often develops over extensive areas, forming an effused pustulate stroma in which numerous clusters of perithecia are developed. These perithecia are collectively erumpent through a small ectostromatic disc. This effused stroma is often bounded beneath by a definite blackened zone.

In this species the grouping of the perithecia has taken place before the entostroma is sharply differentiated and while it still forms effused patches. It differs from such bark-inhabiting species of *Eutypa* as *E. ludibunda*, which may have clustered perithecia, only in the somewhat more strongly developed entostroma and in the blackening of the lower bark tissues. The formation of the clustered perithecia within an effused entostroma is typical of the simpler forms of stroma found in the genera *Eutypella* and *Cryptovalsa*. Although this species shows only a weakly developed ectostroma and has its perithecia collectively erumpent, it possesses an imperfect stage similar to that of the species of *Diatrype*.

This imperfect stage is given by the Tulasnes (123, p. 105) as *Naemospora crocea* (Pers.) Moug. & Nest., or *Libertella faginea* Maz., and is figured (Pl. XII, figs. 18, 19) as having elliptical or irregular cavities within an ectostroma. In the writer's cultures on twigs, the conidial stroma was always ectostromatic. Practically the entire stroma was used up in spore-formation, leaving an open cavity within a slight basal stroma. There sometimes remained a central dome-shaped projection of this basal portion of the stroma (127, Pl. XXI, fig. B, 4). The conidia are filiform, hyaline, curved, and $13-20 \times 0.5-1 \mu$.

This species therefore shows a stromatic structure intermediate between *Eutypa* and *Eutypella*, but with a conidial stage similar to that found in *Diatrype*. Forms similar to this might easily have given rise to the following series by an increase in the number of spores formed in the ascus.

Second Series

The most outstanding character of this second series is the polysporous condition of the asci. This polysporous condition has apparently arisen as the result of an increase in the number of divisions of the nuclei in the ascus, and therefore is derived from the 8-spored condition. Petrak (94, p. 227) has claimed that the species of the genus *Valsella* with polysporous asci are not even specifically distinct from certain species of the subgenus *Leucostoma* which have 8-spored asci. Sydow's *Myc. Germ.* no. 2132, of *Valsa translucens* (de Not.) Ces. & de Not., is an example of this identity, showing both the 8-spored and the many-spored asci in separate stromata of identical structure.

The two genera, *Cryptovalsa* and *Diatrypella*, of this series are, however, distinct from the 8-spored forms. There are two possibilities as to the origin of this polysporous group of species. Either they have a common origin and show a development of their own, or they have arisen from a number of different species or genera by the increase in the number of spores in the ascus. At first glance the latter seems to be the case, for there are species which superficially resemble both *Eutypella* and *Diatrype*. A detailed examination of the two genera shows, however, that they consist of a series of species showing a gradual development from the effused to the isolated type of stroma. The individuals of this series, furthermore, show a closer relationship to one another than to any of the 8-spored genera. The polysporous forms are considered here, therefore, as a monophyletic series.

This polysporous series presents a type of development intermediate between that of *Diatrype* and that of *Eutypella*. The structure of the entostroma is that of the *Eutypella* series, but the conidial stage is usually ectostromatic, and in that respect similar to that of the *Diatrype* series. As pointed out under the discussion of *Quaternaria Persoonii*, this series can be conceived as originating from forms similar to that species.

Cryptovalsa

This genus includes the species with the more primitive type of stromatic development and is only arbitrarily separated from *Diatrypella* upon the basis of its more effused stroma.

The most primitive polysporous type observed by the writer is one collected on *Cercis canadensis* L. This species has the same spore and ascus measurements as *Cryptovalsa sparsa* E. & E., but shows a different stromatic structure. The perithecia are scattered singly or in pairs; they arise in the

bark tissues, but become partially or almost wholly sunken in the wood at maturity. Just above the perithecial initials there occurs a blackening of the bark tissues. Some of the hyphae in this region penetrate into the periderm and weaken that tissue. The growing perithecial necks penetrate the periderm at these weakened points. The blackened zone extends downward to the wood surface, where it spreads out between the perithecia in the lower bark layers. There is very little entostromatic development and practically no ectostroma, and the dorsal blackened zone is the only evidence of a stroma.

This species shows the occurrence of the polysporous condition of the ascus at a level even lower than that of *Quaternaria*.

Cryptovalsa sparsa E. & E. has a somewhat more advanced type of stroma, and resembles *Quaternaria Persoonii* in many respects. The entostroma is weakly developed, usually effused, and outlined at its margin by a blackened zone. The lower bark tissues are often strongly blackened and disintegrated. The perithecia occur singly or in small clusters of 2 to 4. Practically no ectostroma is produced above the perithecial clusters.

Cryptovalsa Nitschkei Fck. was carried in pure culture by the writer, and its development has been described in a previous paper (130). This species has a more strongly differentiated entostroma than *C. sparsa*. The entostromatic areas are usually effused and contain a number of perithecial clusters, although isolated stromata occasionally occur with only one group of perithecia. The marginal zone is here sharply defined. In this species, as in the two preceding, there is merely a slight development of blackened hyphae in the surface bark layers above the perithecia. Some of these hyphae penetrate the periderm and weaken it sufficiently to allow the perithecial necks to rupture this tissue. It is interesting to note that in culture, however, this species produced well developed erumpent ectostromata which were yellow in color. This formation of ectostromata we shall find occurring normally in the higher members of this series. In culture the conidia were formed in labyrinthiform locules within the ectostromata. There was sometimes a strong development of entostromatic mycelium in the surface layers of the bark cells just beneath the ectostromata. These two tissues often formed a more or less homogeneous mass, giving the appearance of an ectostroma partially sunken in the bark. When this was the case, the conidial locules often extended into the entostromatic portion of this tissue. Such a fusion of the ectostromatic mycelium with an entostromatic mycelium in the surface layers of the bark, and a consequent extension of the conidial locules into the entostromatic portion of this tissue, will be found to be characteristic of this series.

Diatrypella

Many species placed in the genus *Diatrypella* have a structure almost identical with that of certain species of *Cryptovalsa*, while others show a

distinctly isolated type of stroma. Three species of this genus have been studied in culture by the writer. We shall first consider a series of species of this genus all of which produce a yellowish-green ectostroma; a character we saw appearing in the cultures of *Cryptovalsa Nitschkei*.

The first species of this series is *Diatrypella quercina* (Pers.) Nit. forma *crataegi* E. & E. (N. A. F. 2d ser., no. 2741). The developmental history of this species has been published by the writer elsewhere (130). This species shows a slightly more advanced type of development than that found in *Cryptovalsa Nitschkei*. The differentiated entostromatic areas are usually effused and contain a number of perithecial clusters. The perithecia are developed beneath small ectostromatic cushions of a yellow-green color. There is often a rich development of entostromatic mycelium beneath these ectostromata, and the fusion of these two tissues gives the appearance of an ectostroma partially sunken in the bark tissue. This is similar to the condition described in *Cryptovalsa Nitschkei*, but it occurs here in nature as well as in culture. The conidial stage consists of an irregular locule in the ectostroma, or occasionally extending into the adjacent entostromatic tissue.

Diatrypella Frostii Pk., which shows another slight advance in stromatic structure, has also been grown by the writer (127). In this species the entostromatic areas are usually isolated, containing only a single group of perithecia. Occasional areas are found, however, with two or more perithecial clusters. A yellow-green ectostromatic disc is usually found above each perithecial cluster. A yellow-green entostromatic mycelium is also produced about the perithecia. In culture there was often no sharp distinction between the ectostroma and the entostroma of the surface bark layers. The conidia were produced in locules within the ectostroma; they were filiform, curved, hyaline, and $30-50 \times 1 \mu$.

Diatrypella betulina Pk. represents the climax type of this series. This species is most interesting in that it presents a structure which is superficially identical with that of a Diatrype, but which has arisen in a different manner. This species has a widely erumpent blackish disc, containing separately erumpent, quadrisulcate, disc-like ostioles. In vertical section the disc tissue is seen to consist entirely of yellowish-green fungous tissue with a blackened surface crust. This greenish tissue originates, however, upon the bark surface beneath the periderm, and is therefore ectostromatic. The ectostroma is, therefore, not deciduous in this case, but forms the erumpent disc itself. The perithecia arise within a hyaline entostromatic tissue in the surface bark layers. These perithecia increase enormously in diameter (to $700-800 \mu$), and in so doing push up the well developed ectostroma and give rise to the strongly erumpent stroma.

The possession in common of a yellowish-green ectostroma by the species of the preceding series might be considered sufficient to place them in a separate group. As this is the only differential character, however, a

thorough investigation of all the polysporous species is necessary before such a separation is made. The following forms have a hyaline ectostroma.

Diatrypella prominens (Howe) E. & E. has isolated entostromatic areas. The hyaline ectostromata are only weakly developed, but the entostromatic mycelium about the perithecia is strongly developed, resulting in a strongly pustulate but only slightly erumpent stroma.

Diatrypella favacea (Fr.) Nit. has been carried in culture by the writer. The details of its development are given in a previous paper (130). The stromata are of the isolated type. The ectostroma is weakly developed and lies chiefly within the periderm itself. The entostroma is strongly developed and causes the pustulate character of the stroma. The ectostroma is not sharply differentiated from the upper entostromatic tissue. The conidial locules are formed within the ectostroma, or sometimes extend into the entostromatic tissue of the upper bark. The conidia are hyaline, curved, and $18-40 \times 1-1.5 \mu$.

Diatrype nigro-annulata (Grev.), *D. Tocciaeana* de Not., and *D. verrucaeformis* (Ehr.) Nit. are all similar in structure to the species just mentioned.

Diatrypella discoidea Cke. & Pk. is another species which imitates a *Diatrype* in appearance. The stromatic structure is similar to that of *D. betulina*, except that the disc tissue is hyaline instead of greenish. In this case, however, remnants of bark cells are found within the disc tissue, and it must therefore be considered as entostromatic in origin. Unfortunately, young stages were not available to the writer for a study of the development of this species. If a well developed deciduous ectostroma is formed in this species, it would be a true *Diatrype* with polysporous asci.

In the preceding discussion of the series with polysporous asci, we have seen that the lower forms of *Cryptovalsa* have a very simple structure. The entostroma is weakly developed, the perithecia are scattered, and practically no ectostroma is formed. As we advanced from the lower to the higher forms, we found a rapid increase in entostromatic development, and a more gradual increase in the formation of ectostromatic tissue. In the genus *Diatrypella* the entostromata become isolated in character. Besides the polysporous condition of the asci, the series is characterized by the fusion of a weakly developed ectostroma with the entostromatic tissue of the upper bark layers. The conidial locules are formed in this tissue, and, although primarily ectostromatic, often extend slightly into the entostromatic tissue below.

The weakly developed ectostroma and the strongly developed entostroma give rise to the characteristic external appearance of the species of this group; most of the species have a strongly pustulate stroma, but a closely adherent periderm and a weakly erumpent disc. Both Füsting (36, p. 186) and Ruhland (99) noticed this correlation between the appearance and the stromatic development of the genus *Diatrypella* and cited this as the differential character between *Diatrypella* and *Diatrype*. The same

appearance and development, on the other hand, are typical of the next series to be discussed.

The climax types of this series, such as *D. betulina* and *D. discoidea*, however, have very well developed ectostromata and widely erumpent discs. This fact was recognized, to some extent, by Ruhland (99, p. 21), who states that *D. quercina* (Pers.) Nit. approaches *Diatrype* in its strongly developed ectostroma.

Third Series: Eutypella

This series includes the single genus *Eutypella*. It is characterized by the 8-spored asci, the small but distinctly differentiated ectostroma, and the conidial locules formed within the entostromatic tissue of the bark. The stromatic configuration in this genus varies from forms with an effused entostroma and more or less scattered perithecia to those with definitely isolated stromata.

Eutypella tumida (E. & E.) Weh. is interesting in this connection in showing almost this entire range of variation within one species. This species was described by Ellis as *Diatrype tumida*. Its life history, as worked out in pure culture by the writer (130), has shown, however, that it is a typical *Eutypella* and not a *Diatrype*. The entostromatic areas are usually effused and contain numerous perithecial clusters or separate perithecia; these areas may in some cases be restricted in area and contain only a single group of perithecia. Numerous small conical ectostromata are formed on the surface of the bark in the effused areas. The perithecia arise singly or in small clusters beneath these ectostromata. The variation in the number and proximity of these ectostromata, and in the number and size of the perithecia formed beneath them, gives rise to a wide range of variation in the outward appearance of the stromatic pustules. In the writer's cultures, the pycnidial locules were sometimes formed within the ectostromata and sometimes in the entostroma of the bark. In nature, the ectostromatic growth not being stimulated as it is in moist culture tubes, the labyrinthiform conidial locules are always formed within the entostromatic tissue of the bark.

Eutypella platani (Schw.) Sacc., *E. fraxinicola* (Cke. & Pk.) Sacc., and other species have a structure very similar to that of the species last named. *E. fraxinicola* has been carried in culture by the writer. Its development is similar to that of *E. tumida* and is described in detail elsewhere (130). Where large erumpent ectostromata were formed in culture, conidial locules developed in this tissue. The imperfect fruit bodies were usually formed in the entostroma, however, and consisted of numerous locules which coalesced to form labyrinthiform chambers. The conidial stage found in nature was also of this entostromatic type.

Other species of *Eutypella* show typical isolated stromata. *E. cerviculata* (Fr.) Sacc., which the writer has studied in culture (129), is an example of this group. The ectostroma of this species is developed largely within the

periderm tissue, the cells of which are split apart over a rather wide area. As a result of this type of growth, a large, rather broadly erumpent stroma is produced, containing many perithecia and a large cluster of well developed sulcate ostioles. In culture the conidial locules were formed within both the ectostroma and the entostroma. The conidia were crescent-shaped, hyaline, and $11-15 \times 1 \mu$. Saccardo (100, vol. 3, p. 602) gives a conidial stage (*Cytosporina cerviculata* Sacc.) similar to this, but with conidia $20-22 \times 0.75 \mu$, as belonging to *E. cerviculata*.

Eutypella angulosa (Nit.) Sacc., *E. alnifraga* (Wahl.) Sacc., *E. similis* (Karst.) Sacc., *E. prunastri* (Pers.) Sacc., and *E. sorbi* (Alb. & Schw.) Sacc. are all similar to, if not identical with, the species last named.

All the species of *Eutypella* thus far mentioned have spores $6-12 \mu$ in length. There is another group of species of this genus which have very small spores ($3-5 \times 1.5 \mu$) and asci ($21-24 \times 4 \mu$). The ostioles of these species tend to be long-cylindrical, sinuous, and almost hair-like, especially when growing under moist conditions. Included in this group are such species as *Eutypella fici* E. & E., *E. capillata* E. & E., *E. scoparia* (Schw.), *E. glandulosa* (Cke.) Ell., *E. microcarpa* E. & E., and *E. exigua* E. & E.

E. fici and *E. glandulosa* have isolated perithecial clusters, but there is no differentiated entostromatic area and the blackened zone is present merely as a continuous blackened crust on the surface of the bark. In *E. scoparia*, on the other hand, there is a well differentiated entostroma, and the marginal zone dips deeply into the bark, cutting off isolated or somewhat effused areas. The writer has examined only three of these species, and it is possible that an examination of other forms would show a developmental series within this group.

The imperfect stage of the genus *Eutypella* is very similar in all cases so far known. It falls in the form genus *Cytosporina*, and from the preceding examples we see that it consists of numerous or labyrinthiform locules formed in the entostromatic masses of mycelium which arise within the bark tissues. Saccardo (100, vol. 3, pp. 602, 603) gives *Cytosporina stellulata* Sacc. and *C. ailanthis* Sacc. as the imperfect stages of *Eutypella stellulata* (Fr.) Sacc. and *E. ailanthis* Sacc., respectively. The Tulasnes (123, p. 187) describe two types of pycnidia for *E. sorbi* (Alb. & Schw.) Sacc. One of these forms, *Cytospora rubescens* Fr., possesses allantoid conidia 3.5μ in length, while the other has the typical filiform conidia, $35-45 \mu$ long. Brefeld (14, p. 240) suggests a relationship between *Eutypella* and *Euvalsa* on the basis of this occurrence of a second allantoid type of conidium in *E. sorbi*. We have seen, however, that *Euvalsa* differs from *Eutypella* in almost every other character. Brefeld failed to obtain fruit bodies of either *Eutypella sorbi* or *E. prunastri* (Pers.) Sacc. in culture.

In his key to the Diatrypaceae, von Höhnelt (60, p. 128) separates the genera *Diatrype* and *Eutypella* on the basis of their imperfect stages; he gives *Diatrype* as having *Libertella*, and *Eutypella* as having *Cytosporina*,

for the conidial stage. We have seen, however, that there are other correlated differential characters in the perithecial stroma.

The structure and the evolutionary development of the stroma in this *Eutypella* series are very similar to what is found in the previously mentioned series with polysporous asci. This series differs, however, in the 8-spored asci, and in the formation of the conidial locules completely within the entostromatic tissues of the bark.

Fourth Series

This series is more heterogeneous than any thus far described. This is true because of the variation of several non-stromatic characters and of the comparatively few transitional species. The apparent relationship of some of the forms here included (*Anthostoma*) to certain of the simple *Sphaeriales* (*Rosellinia*, *Anthostomella*) also makes certain of the suggestions in the following outline more or less tentative. A further study of the life histories and development of a number of these species is needed either to confirm or to alter these suggestions.

The structure of the perithecial centrum in all the species included here is, however, typical of the *Allantosphaeriaceae* (certain species of *Valsaria*, to be considered later, are exceptions to this statement). There are also certain definite evolutionary tendencies in this group. The spores, for instance, show tendencies to become dark-brown, straight-cylindrical or inequilaterally ellipsoid, and uniseriately arranged in the ascus. The asci likewise become cylindrical and shorter-stalked, and there is an increase in the number of filiform hyaline paraphyses. The stromatic development of this series is almost entirely entostromatic, showing an almost entire reduction of the ectostroma.

Cryptosphaeria

Several species of this genus show the origin of brown cylindrical ascospores. As has already been pointed out, the only tissue in *C. populina* which can be considered as ectostroma is a blackened sclerotial layer on the surface of the bark. Paraphyses are rather abundantly present in its perithecia, but the spores are still yellowish-hyaline, allantoid, and biseriately in the ascus. It shows in other words the main features, but none of the variations, of this series.

Cryptosphaeria vicinula (Nyl.) Karst. shows the next step in the development of this series. This species has the same stromatic structure as *C. populina*, but the stromata are more strongly raised and show a tendency to break up into smaller patches. The spores of this species are brown, one-celled, nearly straight-cylindrical or slightly curved, and somewhat larger than those of *C. populina*; they are irregularly biseriately to uniseriately in the ascus.

A specimen of this species on *Alnus*, examined by the writer, shows

stromata less strongly raised above the substratum, and in still more restricted areas. The spores of this specimen were also larger and straighter than those on *Populus*, showing a further development of this tendency. These two forms show the transition from the yellow-hyaline, allantoid, biseriata condition of the ascospores to the dark-brown, straight-cylindrical, uniseriate type. Let us now examine several species which show the tendency towards the septation of the ascospore.

Cryptosphaeria millepunctata Grev. (*Endoxyla fraxini* E. & E.) is a species with an effused entostroma which possesses septate ascospores. This species has been carried in culture by the writer, and its life history is given in a previous paper (129). The entostroma is widely effused, occupying the entire upper portion of the bark tissue over wide areas; the lower bark tissues are heavily blackened. In nature no ectostroma is formed. There is only a slight blackening of the bark tissue about each of the separately erumpent perithecial necks. The conidial locules, in nature, are labyrinthiform, and formed with the perithecia in the entostromatic tissue of the bark. In culture, ectostromatic cushions were formed on the bark surface and conidial locules were produced within these stromata. The conidia were filiform, curved, hyaline, and $30-40 \times 1 \mu$. A second, shorter type of conidium, $13-20 \times 1 \mu$, was formed in twig cultures. The spores of this species are quite variable; they are hyaline, allantoid, and one-celled when young, but become dark brown, 1- to 4-septate, and nearly straight cylindrical at maturity. They are biseriata in the ascus. Brefeld (14) grew this species and noted that the spores became 1- to 3-septate upon germination. The writer has also observed the non-septate spores become 1- to 5-septate, and constricted at the septa upon germination. Brefeld reported the formation in culture of free conidiophores on stromatic cushions, as well as the production of conidial locules within these stromata.

This species shows the occurrence of septate spores in a member of this series with an effused stroma. The formation of conidial locules in the entostroma is characteristic of all the known imperfect stages of this series.

Valsaria

The relationships of this genus are difficult to determine. As it stands today it contains species belonging to both the Allantosphaeriaceae and the Diaporthaceae.

There are two species, the structure of whose perithecial centrum is that of the Allantosphaeriaceae. The spores of these two species are undoubtedly derived from the allantoid type, and their stromatic development is similar to that of *Anthostoma*.

The first of these species, *Valsaria moroides* (Cke. & Pk.) Sacc., has a strongly pustulate stroma, but the disc is scarcely erumpent. Isolated, differentiated, entostromatic areas are formed, but these are not bounded by any dark marginal zone. There is no ectostroma formed, and the

rupturing of the periderm takes place in a manner characteristic of both *Valsaria* and *Anthostoma*. There is a blackening of the hyphae in the surface layers of the bark, and some of these hyphae penetrate into the periderm and weaken this tissue. The growth of the perithecial necks and of this mass of entostroma bursts open the periderm at the point weakened by the penetration of the hyphae mentioned. The spores of this species are variable; they are irregularly biseriate to uniseriate in the ascus, either straight-cylindrical or allantoid, brown in color, contain 2-6 yellowish areas, and are uniseptate at maturity. Both the straight-cylindrical and the allantoid spores are constricted at the septum.

The second species with spores of an allantoid character is *Valsaria allantospora* E. & E. (31, p. 343) (*V. coloradensis* E. & E.; 32, p. 342). *V. moroides* var. *aceris* Rehm (U. S. Dept. Agr. Myc. and Path. Coll. no. 1687) is an immature specimen of this species. The entostromatic area in this case is light in color, often somewhat effused, and bounded by a definite blackened zone. The rupturing of the periderm is similar to that in the preceding species. The spores are biseriate, dark brown, and vary from the allantoid non-septate to the straight-cylindrical septate condition; they are not constricted at the septum.

Unfortunately, the writer has been unable to obtain the two last-named species in culture, and their imperfect stage is apparently unknown. The spores of these species show a clear relationship to the allantoid forms. The remaining species of the genus, which should be considered the true *Valsarias*, have broad elliptical-fusoid spores; they are dark brown, uniseptate, constricted at the septum, and are not at all characteristic of the *Allantosphaeriaceae*.

The position of these species is somewhat doubtful. Such species as *Valsaria insitiva* Ces. & de Not. and *V. exasperans* (Ger.) E. & E. show many characters similar to those of the genus *Anthostoma*. A close examination of the perithecial centrum and of the character of the spores, however, indicates their relationship to be with the *Diaporthaceae*, probably near *Endothia*. In those species of the *Diaporthaceae* which have numerous persistent paraphyses, the asci are held within this mass of paraphyses and appear as a definite, persistent, hymenial layer, similar to that formed in the *Allantosphaeriaceae*. This is the case in these species of *Valsaria*. The attachment of the asci in these species, however, is seen to be by a short, stout, somewhat curved base, which is characteristic of the *Diaporthaceae*, while in *V. moroides* and *V. allantospora* the base of the ascus consists of a short but narrowly tapered stipe, which is typical of the *Allantosphaeriaceae*.

The method of rupturing the periderm is similar in *V. insitiva* and *V. exasperans* to that in the rest of the species of this series. In *V. insitiva* there is a rapid proliferation of black-walled hyphae in the upper bark layers. The bark cells are absorbed by, or become imbedded within, this tissue, which ruptures the periderm and forms an erumpent disc. This is

a purely mechanical tissue, for many such discs are formed which have no perithecia formed beneath them. A blackened zone extends downward from this disc and surrounds the perithecial cluster.

In *V. exasperans* an area of the upper bark tissues is early cut off by a darkened marginal zone. A rapid proliferation of entostromatic hyphae takes place within this enclosing zone. The perithecia arise within this tissue, and its subsequent growth produces a large erumpent stroma, composed largely of grayish-hyaline hyphae, within which the remnants of the bark cells are imbedded.

From what has been said we see that these two *Valsarias* have a purely entostromatic development similar to that found in *V. moroides* and *V. allantospora*.

Both *V. insitiva* and *V. exasperans* have been grown by the writer, and their life histories have been published (1927). As usual, in culture the growth was superficial, and large erumpent stromata were produced which were apparently ectostromatic. In both species the conidial locules were labyrinthiform, and were formed in such stromata. In nature the imperfect stage of *V. insitiva* was found in the same entostroma with the perithecia. In *V. exasperans* the conidial stage occurred in separate entostromata, identical with the perithecial stromata. The conidial locules are therefore entostromatic in these species also. The conidia, from culture, were minute, elliptical, one-celled, and hyaline. These conidia differ from any so far found in the Allantosphaeriaceae. The Tulasnes (123, Pl. XI, figs. 13, 16) figure a similar conidial stage for *V. rubricosa* (Fr.) Sacc. Ruhland (99) studied the development of *V. rubricosa*. In spite of the fact that he distinctly states that the stroma of this species arises as a proliferation of hyphae within the bark, he places it in his "haplostromatic" series, which type of stroma he in turn considers as being entirely ectostromatic. This illustrates the confused notion of these two types of stromatic tissue held even by Ruhland himself.

From our discussion of the genus *Valsaria*, it seems that, although it has the stromatic development of an *Anthostoma*, it is in reality more closely related to *Endothia*. This may be considered as another case of an analogous type of structure arising in two widely separated series. We have emphasized here the similarities between *Valsaria* and the other forms of this series. Following the discussion of *Endothia* we shall consider its relationship to that genus.

Anthostoma

We now come to the genus *Anthostoma*, which is characterized by its one-celled, brown, cylindrical or inequilateral ascospores. We have seen that certain species of *Cryptosphaeria* show a transition from the allantoid yellow-hyaline ascospore to the brown cylindrical type. Such transitional forms, as well as other characters soon to be discussed, suggest the origin of the *Anthostoma* group from allantoid-spored forms. Such a hypothesis

would unify the entire group of the Allantosphaeriaceae. It would overlook entirely, however, another fact, namely, that there is a long series of forms extending back into the simple Sphaeriales which show an identical spore form, and which seem undoubtedly related to Anthostoma. The reference is to such genera as Anthostomella and Rosellinia. The entire family of the Xylariaceae, furthermore, is characterized by the same spore form and can be considered a further development of the Anthostoma type. In fact, this evidence is so convincing that it seems probable that such a series might constitute a third large group, comparable to the two here considered under the stromatic Sphaeriales. Petrak (94, p. 253) has already suggested the relationships of these forms. Very little is known of the life histories and development of the lower forms of this hypothetical series, however, and such knowledge must first be obtained before any conclusions can be drawn. Let us first consider what evidence we have.

The genus Anthostoma was divided by Nitschke (83) into two subgenera, Euanthostoma and Lopadostoma. The subgenus Euanthostoma consists of effused forms, which usually inhabit decorticated wood. Such forms are closely related to the simpler forms found in Anthostomella, where the perithecia are more scattered, and with a separate blackened "clypeus" about each perithecial neck. Unfortunately, material of these species has not been available to the writer, either for culture or for study. Their relationships, therefore, must be omitted in the present discussion.

Anthostoma decipiens (DC.) Nit. is an effused form, which was described and figured by the Tulasnes (123, Pl. VIII, figs. 1-8) as an Eutypa. This species is figured as having labyrinthiform conidial locules formed within the entostroma; the conidia are hyaline and allantoid. Free conidiophores bearing similar conidia are also figured. This imperfect stage is strikingly like those previously noted in the genus Eutypa.

Petrak (94, p. 254) separated the subgenus Lopadostoma into two groups. He has made this separation of the entire subgenus, apparently, upon the study of two species only. He gives *A. turgidum* (Fr.) Nit. as an example of the first group, and *A. gastrinum* (Fr.) Sacc. as typical of the second group. *A. microsporum* Karst., which he also mentions, he places in neither group. The only character for the basis of such a separation that the writer can see is the presence or absence of the dark marginal zone.

Anthostoma turgidum (Fr.) Nit., which typifies Petrak's first group without a marginal zone, has a stromatic structure similar to that of *Quaternaria Persoonii*. The small perithecial clusters are scattered in the light-colored upper layers of the bark, while the lower bark layers are blackened and disintegrated. The periderm is ruptured by the mechanical force of the growth of the fused ostioles.

Diatrype dryophilum Curr. var. *minor* Grev. (N. A. F. no. 87), which was later recognized by Ellis (29, p. 581) as an Anthostoma, also belongs in this group. The periderm is ruptured by the massed ostioles, and the surface of the bark is blackened, but there is no bounding zone in the bark.

Anthostoma microsporum Karst. shows a well differentiated entostroma of blackened tissue, but no black marginal zone.

Anthostoma gastrinum, characteristic of the second group, has light-colored entostromatic areas, which are often somewhat effused and are always bounded by a darkened zone. The periderm is ruptured by the growth of a mass of blackened tissue, composed of the fused perithecial necks and an entostromatic tissue formed in the surface bark layers.

Diatrype phaeosperma Ell. [*Anthostoma phaeosperma* (Ell.) Sacc.] (N. A. F. no. 1557) is a form with isolated entostromatic areas and a blackened bounding zone. The superficial appearance of the stroma of this species is that of a *Diatrype*. Its internal structure is identical with that described for *Diatrypella discoidea*; that is, the disc tissue is composed of a well developed entostromatic tissue with a darkened superficial crust. In the case of this species, an examination of young stages has shown that no ectostroma is formed and that the development of the entostroma itself ruptures the periderm. The spores of this species, although dark-brown, are slightly but distinctly allantoid. In this respect this species is similar to *Quaternaria Morthieri*, which we have already seen should in reality be placed in the genus *Anthostoma*. *Q. Morthieri* has a stromatic structure almost identical with that of *A. turgidum* and would fall in the first group.

Anthostoma juglandinum Rehm var. *caryae* Rehm (98) also belongs in this second group. It has effused entostromatic areas, with a marginal zone. The rupture of the periderm is similar to that found in the rest of the genus.

The conidial connections of the subgenus *Lopadostoma* are not very well known. Nitschke (83, p. 121) states that the conidial stromata of *A. turgidum* are Cytospora-like, containing numerous locules in which are formed allantoid, hyaline conidia, $10 \times 1.5 \mu$. Brefeld (14, pp. 241, 242) grew *A. turgidum* and *A. Xylostei* (Pers.), but obtained only sterile mycelium. Fuckel gave *Myxosporium sanguineum* as the conidial stage of *A. gastrinum*, but Winter (132, p. 759) considers this doubtful.

From the preceding discussion it seems certain that many species of *Anthostoma* have arisen from forms with allantoid spores. *A. decipiens* shows the hyphomycetous stage characteristic of the genus *Eutypa*, as well as the entostromatic pycnidial stage typical of so many of the allantoid-spored genera. *A. phaeosperma* and *Quaternaria* (*Anthostoma*) *Morthieri*, as we have seen, have distinctly allantoid spores. *A. turgidum* has been reported as having a conidial stage typical of the *Allantosphaeriaceae*.

How, then, can we harmonize these facts with the existence of a continuous series of forms, from *Rosellinia* through *Anthostomella* and, supposedly, *Anthostoma* to *Hypoxylon* and the *Xylariaceae*? There are two possibilities. Either there are two separate series, or the *Allantosphaeriaceae* have arisen from the series of forms with brown cylindrical ascospores. The writer hesitates to make this latter suggestion, because it involves the

origin of light-colored spores from darker-colored ones, which is the reverse of what generally seems to be true of the evolution of the spores in other groups. This view is particularly tempting because of the lack of any definite series of allantoid-spored forms in the simple Sphaeriales, from which the Allantosphaeriaceae could be derived. This does not explain the fact, however, that the lighter-colored spores usually occur in those species of the Allantosphaeriaceae with the simpler stromatic structure. It is the writer's opinion, rather, that further study of these forms will reveal two groups of brown-spored forms. One of these will consist of the Rosellinia—Anthostomella—Xylariaceae series; and the second will consist of forms related to, and derived from, the Allantosphaeriaceae. Only a further study of the life histories of a number of these species will determine what differential characters can be used to distinguish these two groups.

Summary (Allantosphaeriaceae)

Let us now review briefly the phylogenetic development of the Allantosphaeriaceae as outlined above. We found the simplest forms to be species of *Eutypa*, living chiefly upon decorticated wood. The perithecia of these forms are scattered singly, but are united by a blackened crust on the surface of the substratum. A primitive hyphomycetous stage is retained in their life history, but they also form conidial locules within a stroma.

The first step in the evolution of these forms was the production of a rich mycelium about the fruit bodies, within the substratum. This soon resulted in the development of a differentiated entostromatic area, bounded by a blackened marginal zone. At this stage in the evolution of the group, we can already discern the four separate lines of development already discussed, since there are effused forms with separately erumpent perithecia in all these series.

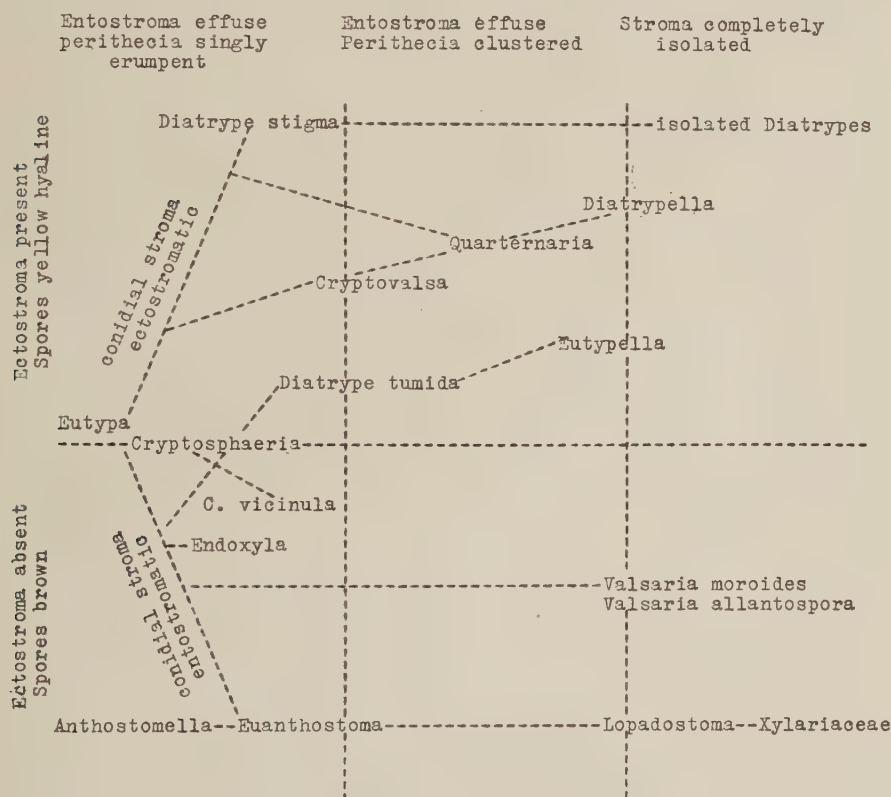
One group of forms (*Diatrype*) has produced, very early in its evolutionary development, a very strongly developed and deciduous ectostroma. The result of the efficient casting off of the periderm by this deciduous mechanical tissue is a characteristic structure. In the first place, the conidial locules are formed within this well developed ectostromatic tissue; in the second place, the perithecial necks, having no resistant tissue to penetrate, remain separately erumpent. Even in the most isolated and well developed stromata of this series, as in *D. virescens* or *D. disciformis*, there is no convergence of the perithecial necks. In this respect this series stands in contrast to all the rest of the family.

In the remaining series there occurs a grouping of the perithecia and a convergence of the perithecial necks, resulting in collectively erumpent ostioles. This clustering of the perithecia takes place along with the development of the entostroma, and we often find numerous perithecial clusters formed within a single effused entostroma. At the same time that this grouping of the perithecia takes place, there is developed above each

group an ectostromatic cushion, or some other type of mechanical tissue to aid in the rupture of the periderm. As soon as the clustering of the perithecia has taken place and a compound fruit body is organized, the development of the entostromatic tissue becomes limited to the area about each cluster of perithecia, and there results a true isolated type of stroma.

Such an evolution of the stroma and the compound fruit body can be traced in that series of forms which have the polysporous ascus as a constant character. In this series there is practically no ectostroma formed in the lower forms, such as *Cryptovalsa sparsa*, but in the higher isolated types of stroma, such as *Diatrypella betulina* and *D. quercina*, this tissue becomes rather strongly developed. The conidial stage of this series is formed primarily in the ectostroma, but, on account of the well developed entostroma in the surface bark layers, the conidial locules may extend somewhat into this tissue.

The two genera *Cryptovalsa* and *Diatrypella* are merely arbitrarily selected portions of the same developmental series. Some species of this group, we have seen, differ from the rest in the yellow-green coloration of the ectostroma.



TEXT FIG. 1. The phylogenetic relationships of the Allantosphaeriaceae.

The genus *Eutypella* has a stromatic development like that of the preceding series. It differs in the 8-spored asci and in the conidial stage, which is here formed primarily within the entostroma although locules may also be occasionally found in the ectostroma.

The fourth and last series is characterized by its entostromatic conidial stage and by the entostromatic character of the tissue which functions in the rupture of the periderm. This series shows the most complete reduction of the ectostroma and the most strongly developed entostroma. In the genus *Cryptosphaeria* there is a tendency toward a coloration, a uniseriate arrangement of the spores, and the formation of numerous paraphyses. In *C. millepunctata*, *Valsaria moroides*, and *V. allantospora* there is a tendency toward both a coloration and a septation of the ascospores, as well as an increase in the number of paraphyses. In the genus *Anthostoma* we find a number of species of a climax type, with brown, cylindrical, uniseriate spores, cylindrical, short-stalked asci, and numerous paraphyses. This genus suggests a relationship with the series of brown-spored forms already mentioned, and needs further study to determine its exact relationships.

The phylogenetic relationships of this family of the Allantosphaeriaceae may be represented diagrammatically as in text figure 1.

Diaporthaceae

The second large group of the stromatic Sphaeriales which shows a common relationship is that belonging to the general type designated by von Höhnelt (59) as the "Diaporthen." The "Diaporthen" are also characterized by the structure of their perithecial centrum. In this group the asci have no definite stalk and do not remain in a definite hymenial layer after maturity, as in the Allantosphaeriaceae. When moistened, the base of the ascus contracts and dissolves, pinching off the ascus from its attachment. The ascus walls are delicate, and break down in water. As a result of these qualities of the ascus, the entire central cavity of the perithecium becomes filled with a mass of free asci and spores, giving the characteristic appearance of this type of perithecial centrum. In many species there is a ring or collar of protoplasm which extends into the thickened apical wall of the ascus, such as is found in *Gnomonia* and related genera. The paraphyses are delicate and numerous in the young perithecium, but are very evanescent. In the mature perithecium they are either absent, or present as a few delicate, broad, band-like filaments. In the higher forms, however, the paraphyses become more numerous, persistent, and filamentous. In these cases the asci may be held in place by the mass of paraphyses, and the appearance of the perithecial centrum is then somewhat different from that of the lower forms. Petrak (92, pp. 65, 68) has designated the band-like evanescent paraphyses as "pseudoparaphyses" and the filamentous persistent structures of the higher forms as "metaphyses."

The spores of this group are various in shape and septation, being elliptical, allantoid, or long-cylindrical, hyaline to colored, and 1- to many-septate.

The imperfect stage is always formed in, or on, an ectostromatic cushion, which in some cases may be intimately associated with a well developed entostroma beneath. The conidia may be formed in enclosed locules, open cavities, or exposed layers. Most of the species have two types of conidia. One type is one-celled, hyaline, and rod-shaped to allantoid or long-cylindrical. The second type varies from hyaline to brown and from one- to many-celled. Three series of development will be considered in this group.

First Series

The first series of related species which we shall attempt to trace in the Diaporthaceae includes the genera Diaporthe, Melanconis, and Pseudovalsa. Starting with the primitive forms, we soon encounter what seem to be two separate lines of phylogenetic development, one of which again seems separable into two groups. These three series culminate in the three genera just mentioned.

The presence or absence of a dark marginal zone about the perithecia in this series seems to be correlated with the type of imperfect fruit body formed. Petrak (94, p. 320) noted that the absence of such a dark marginal zone distinguishes the genus Melanconis, with dark-colored conidia, from the genus Diaporthe, which has hyaline conidia. There seem to be, however, certain species, as for example those in Petrak's (89, p. 117) genus Cryptodiaporthe, which lack a dark zone and yet have hyaline conidia. These facts can be established only by further cultural studies. For convenience, however, the species without such a marginal blackened zone will be spoken of as the Melanconis group, while those possessing such a zone will be spoken of as the Diaporthe group.

The evolution within this group shows the gradual development of a number of characters along several diverging lines. There is a general tendency throughout towards the development of a stroma and the clustering of the perithecia. There is also an increase in the number and persistence of the paraphysis-like structures, although the data concerning this character are still somewhat vague and conflicting. The spores in the lower forms are all 2-celled and hyaline. In the Diaporthe group the spores remain hyaline; in the genus Melanconis the spores become brown in the higher forms; while in Pseudovalsa they become brown and many-celled. In most species the spores are biseriate in the ascus, but in some species of Melanconis they become uniseriate. In the Diaporthe group the conidia are hyaline and non-septate, and are formed within pycnidial locules; in the Melanconis group the conidia tend to become colored and septate, and the hymenial layers tend to become more exposed. In the genus Melanconis the conidia remain non-septate and brown, while in the genus Pseudovalsa they become septate and brown.

Diaporthe

The genus *Diaporthe* includes an unusually large number of named species, many of which are undoubtedly synonymous. There remain, however, a large number of species within a comparatively small range of variation, resulting in almost every conceivable combination of characters. The only constant character is the 2-celled hyaline spore. If we add to this character the presence of a dark marginal line and of a Phomopsis stage in the life history, we delimit a compact, related group which can ultimately represent the natural outlines of the genus *Diaporthe*.

The origin of the simpler forms of the genus *Diaporthe* from the genus *Gnomonia* is so evident that it is unnecessary to go into detail in this respect. Species such as *D. rostellata* (Fr.) Nit. resemble a typical *Gnomonia* in every way, and have been placed in the genus *Diaporthe* only because of their stem-inhabiting character. The distinction, previously mentioned, between the *Diaporthe* group and the *Melanconis* group of this series can not be traced with any assurance in the lower forms. In certain *Euporthe* forms, as for example, *D. exercitalis* (Pk.) Sacc., the only evidence of a stroma is that furnished by the thickly scattered perithecia, while others with similarly scattered perithecia show, in addition, a blackening of the surface of the substratum. Further connections of perfect and imperfect stages are needed to show any relation of these forms to the two groups mentioned.

The compound fruit bodies in this genus have arisen as the result of two tendencies: the development of a stromatic mycelium, and the clustering of the perithecia. Nitschke's (83) division of the genus into the three subgenera *Euporthe*, *Tetrastaga*, and *Chorostate* draws arbitrary lines directly across these two tendencies and, as von Höhnelt (57, p. 382) has remarked, is an unnatural division. A single species may show a variation over the range of all three subgenera. *D. fasciculata* Nit. in the subgenus *Euporthe*, and *D. oncostoma* (Duby) Fck. in the subgenus *Chorostate*, for instance, are identical. The position of the perithecia within the wood tissue (*Euporthe*) in many species inhabiting herbaceous stems is merely due to a lack of sufficient bark cortex for these fruit bodies. This is shown by the fact that where a sufficient cortex is developed (as noted by the writer in the cases of *D. euspina* (Cke. & Ell.) Sacc. on *Chenopodium* and *D. aculeata* (Schw.) Sacc. on *Phytolacca*) the perithecia may develop partially or entirely within this tissue.

The development of the stroma and the clustering of the perithecia take place independently in the various species. As already noted, the first appearance of the stroma is a blackening of the surface of the substratum, as seen in *D. arctii* (Lasch.) Nit., *D. euspina* (Cke. & Ell.) Sacc., etc., which show no clustering of the perithecia. In other species, as *D. densissima* Ell. and *D. salicella* (Fr.) Sacc., there is a tendency toward a clustering of the perithecia, or at least a convergence of the necks of neighboring perithecia

so as to become collectively erumpent, without any evidence of a marginal zone. Such species show a possible origin of the Melanconis group. Petrak (90, p. 180) gives the imperfect stage of *D. salicella* as *Discella carbonacea* (Fr.) Berk. & Br., which he considers a Septomyxa, and which has 2-celled hyaline conidia. This connection was by observation only, and the same *Discella* was previously given by Petrak as the imperfect stage of *Diaporthe tessella* on the same basis. Such information is of course usable only as a suggestion until verified by culture, but if true such an imperfect stage would be characteristic rather of those forms of the Melanconis group related to *Pseudovalsa*, as will be brought out later.

Such species as *D. Woolworthii*⁴ (Pk.) Sacc. and *D. ulmicola* E. & E. show a clustering of the perithecia and also a darkened zone on the surface of the bark tissues. *D. ulmicola* also shows the beginning of the formation of an entostromatic mycelium within the bark tissue. In the *Diaporthe* group, as this development of an entostromatic mycelium increases in amount, there is usually formed a differentiated entostromatic area, which is surrounded by the characteristic blackened marginal line.

There are a few species which develop such a differentiated entostromatic area and retain the separately erumpent character of the perithecia. *D. decedens* (Fr.) Fck. shows a tendency for its perithecia to become clustered and often shows a faint darkened zone about the clusters, but the perithecia remain separately erumpent. In *D. tessella* (Pers.) Rehm, the perithecia are grouped in a slightly differentiated entostromatic area bounded by a definite dark line, but the perithecia are separately erumpent. In *D. sociata* (C. & E.) Sacc., the perithecia are within a strongly differentiated area, bounded by a blackened zone which dips deeply into the wood. The surface of the bark is heavily carbonized between the perithecial necks, forming a blackened "clypeus." In spite of this high development of the stroma, the perithecia have remained separately erumpent.

The majority of the species of the *Diaporthe* group with differentiated entostromatic areas have the clustered perithecia collectively erumpent. The configuration of this entostromatic area may be various. In some species each perithecial group is imbedded in an isolated entostromatic area, as in *D. oxyspora* (Pk.) Sacc., which may or may not be connected with its neighbors by a continuation of this marginal zone. In other cases the entostromatic areas may be more or less effused and contain a number of perithecial clusters, as in *D. impulsula* (Cke. & Pk.) Sacc., or the perithecia may occasionally be somewhat scattered. The marginal zone may be only dorsal, as in *D. detrusa* (Fr.) Fck., and delimit the upper surface of the area only, or it may also be ventral and dip into the wood, outlining the stromatic area beneath, as in *D. tuberculosa* (Ell.) Sacc. These stromatic characters often vary widely within the same species, as in *D. acerina* (Pk.) Sacc., and can be used only with an understanding of the specific variations.

⁴Given as *Valsa Woolworthi* by Peck (N. Y. State Mus. Rept. 28: 73). Spelling changed to *D. Woolworthii* by Saccardo (Syll. 1: 615).

Ruhland (99) considered the stromatic development of the two Chorostate forms which he studied to be intermediate between his "entoplacodial" and "ectoplacodial" types, because the erumpent disc is of ectostromatic tissue but is often obliterated by the growth of the erumpent ostioles. In general the development of ectostromatic tissue is less distinct in the species of the Diaporthe group than in those of the Melanconis group. In the simpler forms the pycnidia are produced in small ectostromatic masses just beneath the periderm, and the scattered perithecia are not oriented in any way in respect to the ectostromata. Where the perithecia are formed in clusters, it is usually beneath these ectostromatic pycnidia. In the higher forms, where an entostromatic mycelium is formed about the perithecia, this ectostromatic disc often remains sterile. In such forms the ectostroma is often not sharply differentiated from the entostroma, and when the pycnidial locules are formed they may be within a stroma which is partially or wholly imbedded within the bark.

For the sake of clearness we shall proceed here to a discussion of the imperfect stages of the Diaporthe group, and discuss the Melanconis group of the genus Diaporthe under the genus Melanconis, in order to bring out the development of what seems to be a separate series of forms.

The imperfect fruit bodies as well as the perithecia of the genus Diaporthe can be derived from the genus Gnomonia. The fact that these imperfect forms have been placed in numerous genera, and even in different orders, of the fungi imperfecti does not disprove their relationship, but rather discloses the artificiality of our classification. Klebahn (67, 69, 72) has given the complete life histories of a number of species of Gnomonia. The imperfect stages of this group consist of thin stromatic patches of mycelium formed within or beneath the cuticle of the host. Upon this basal hymenium is borne the hymenial layer that produces the conidia, which are hyaline, usually one-celled, and elliptical to rod-shaped. In *G. leptostyla* (Fr.) Ces. & de Not. (69), both one-celled, rod-shaped, and 2-celled, crescent-shaped conidia are formed. The probable relation of these 2-celled spores to the septate conidia of certain species of the Melanconis group will be discussed later. The presence of the two types of conidia is common to the genera Diaporthe, Melanconis, and Pseudovalsa.

The classical paper of Klebahn (67) on *Gnomonia veneta* (Sacc. & Speg.) Kleb. (*G. platani* Kleb., or *Apiognomonium veneta* (Sacc. & Speg.) v. H.) points out the tendency toward the formation of a greater amount of stromatic mycelium in the production of the conidial fruit body. On leaves this fungus produces a typical Gloeosporium (*Gl. nervisequum* (Fck.) Sacc.). On dead fallen leaves, a pycnidial stroma more or less imbedded within the leaf tissue is formed, which is known as *Sporonema platani* Baumler, or *Fusicoccum veronense* C. Mass. On twigs the hymenial layer is formed in a cavity beneath a lenticel. On account of the resistance of the overlying cork tissues, this layer is not ruptured widely, and the locule beneath is

lined with the hymenium and the underlying mycelial layer. This fruit body, known as *Discula platani* (Pk.) Sacc., differs from the typical *Phomopsis* of the lower forms of *Diaporthe* only in the slight presence of the outer stromatic wall and in the lack of the two types of spores.

The *Gnomonia* just mentioned is one with unequally 2-celled ascospores, and is placed by von Höhnelt in the genus *Apiognomonina*. *Diaporthe obscura* (Pk.) Sacc., which has been grown in culture by the writer (129), also has unequally 2-celled ascospores and would fall in von Höhnelt's genus *Apioporthes* (57, p. 381). This species has a strongly developed stroma and produces stromatic pycnidia (129, Pl. III, figs. 3, 6), within which are produced conidia that vary in shape from elliptical to cylindric-fusoid and suggest strongly the differentiation into two types of conidia.

The imperfect stages of the species of the *Diaporthe* group are strikingly constant, being, almost universally, species of the genus *Phomopsis*. The species of the *Melanconis* group on the contrary have their conidia borne in open cavities or layers, and one type of conidium is dark-colored, or septate, or both. An examination of the various species of *Diaporthe* connected with the genus *Phomopsis* in Diedicke's (23) article on the latter genus brings out this correlation in a striking manner. Of the 74 specific connections reported by Diedicke, there is only one, *D. leiphaemia*, which belongs to the *Melanconis* group. The connections of this species with its imperfect stage seem to be somewhat confused, but judging from the opinion of Diedicke (23), the figures of the Tulasnes (123, Pl. XXIII, figs. 5-10), and the discussion of von Höhnelt (57), the imperfect fruit body is apparently transitional between *Phomopsis* and *Fusicoccum*. Several of the species mentioned by Diedicke are of the subgenus *Euporthes* and have no dark line; one, *D. vepris* (de Lacr.) Fck., is in reality a *Gnomonia* according to Winter (132, p. 637); and one, *D. nigrella* (Auers.) Niessl., has one-celled spores and belongs to the genus *Diaporthopsis* Fabre (Ann. Sci. Nat. Bot. VI, 15: 35); but all the remaining species are typically of the *Diaporthe* group. The imperfect fruit body of these *Phomopsis* types consists of a spherical, flattened, or somewhat irregular cavity, which is formed within a more or less well developed ectostroma. This ectostroma may occur isolated, or in connection with a perithecial entostroma beneath. There are two types of spores formed, either in separate pycnidia, or usually in the same pycnidium. One type of conidium is long-cylindrical, hyaline, one-celled, and usually curved or hamate; the other type is one-celled, hyaline, elliptical to fusoid, and contains two oil droplets, which von Höhnelt (51, pp. 681, 682) considers an indication of a tendency toward the formation of septate conidia.

The writer has carried five species of this *Diaporthe* group in culture (*D. oncostoma* (Duby) Fck. (127), *D. faginea* (Curr.) Sacc., *D. pruni* E. & E., *D. sp.* and *D. binoculata* (Ell.) Sacc. var. *ilicis* (128). The first four produced typical *Phomopsis* fruit bodies. *D. binoculata* formed the long-hamate type

of spores in a locule above the perithecial fruit body and the shorter fusoid to cylindrical spores in isolated stromata, which sometimes had more or less exposed cavities.

From the preceding it is seen that in this *Diaporthe* group as here limited we have a correlation between the occurrence of a dark marginal line about the perithecial stroma and the formation of a typical *Phomopsis* fruit body in the conidial stage of the life history.

Melanconis

When one comes to consider that group of species of the genera *Diaporthe*, *Melanconis*, and *Pseudovalsa* without a dark marginal zone, one is impressed with the idea that he is here again dealing with two lines of development.

The stromatic development of these forms is of two types. Many species have a sharply defined, truncate-conical, well developed ectostroma, but practically no entostroma that can be recognized as such; the perithecia are buried in a circinate manner about this central disc in the unaltered bark cortex. A second group of species has no such sharply defined ectostromatic disc. They either show very little stromatic development at all, or, where a stromatic mycelium is developed, it is found in the bark tissues between the perithecial necks, or extending down between the perithecia themselves. There seems, furthermore, to be a correlation between these two types of stroma and the type of imperfect stage produced. The group first mentioned, with a definite ectostroma, has, as a rule, one-celled dark-colored conidia, and represents the genus *Melanconis*. The second group, as far as the evidence goes, has septate, hyaline to colored conidia, and includes the genus *Pseudovalsa*. It must be admitted that the evidence for such a separation is as yet fragmentary and that certain exceptions exist, but let us consider this evidence. Since the old classification cuts across these apparent lines of development, it will be necessary under the discussion of *Melanconis* and *Pseudovalsa* to consider species which have in the past been placed in various other genera. As the possession of dark-colored one-celled conidia has always been considered a character of the genus *Melanconis*, we shall here consider the series of forms possessing this character.

The *Melanconis* group of the genus *Diaporthe* includes such species as *D. marginalis* Pk., *D. albovelata* (B. & C.) Sacc., *D. galericulata* (Tul.) Sacc., *D. Ellisii* Rehm, *D. decipiens* Sacc., and others. The perithecial stroma of these species can be distinguished in no way from the hyaline-spored forms placed in the genus *Melanconis*. The juggling back and forth of many of these species between the two genera shows their position to be mainly one of personal opinion. The presence of dark-colored one-celled conidia (*Melanconium* stage) has been used as a criterion for the separation of these species. Culture experiments of the writer have shown that both *D. marginalis* and *D. albovelata* (127) have dark-colored conidia, and Graves

(38) has transferred the old *Diaporthe juglandis* E. & E. to the genus *Melanconis* on the basis of similar cultural results. It will probably be shown that most of these species of the *Melanconis* group of the genus *Diaporthe* have dark-colored conidia.

Many of these species with a *Melanconium* stage in their life history have a distinctly yellowish or olive-colored ectostroma. The ascospores of this group tend to become colored and lie uniseriately in a cylindrical ascus, especially in the higher forms. The conidial stroma in most cases is that of a typical *Melanconium*. The conidial hymenium, instead of being borne in an enclosed locule as in the *Phomopsis* type belonging to the *Diaporthe* group, is here borne in open cavities. The well developed ectostroma ordinarily bursts through the periderm as a sterile disc. The conidial hymenium is formed in shallow cavities upon the slanting sides and bases of this stroma. In vertical section such a fruit body shows two lateral cavities on either side of the central sterile disc. In some cases in which the growth is rapid, the hymenium develops over the entire surface of the ectostroma before it bursts through the periderm, and as a result it appears in vertical section as a single cavity arched over by the periderm; the undeveloped sterile disc appears as a central dome-shaped projection. If the periderm is widely ruptured the spores are emitted as a mass, while if only a small pore is formed they emerge as a spore horn. This stromatic configuration may vary for one and the same species under different growth conditions. Perithecial stromata may or may not form beneath these conidial ectostromata.

Let us consider a few species which illustrate the development of this group. *D. marginalis* Pk. is a species with hyaline appendiculate ascospores which are biseriate in the ascus. The definite conical ectostromatic disc of this species is white in color. In the writer's cultures (unpublished) it has produced one-celled, elliptical, dilute-blackish conidia, with which were mixed a second type of cylindrical hyaline conidia. The conidial mass is black in color. The conidia are formed on the lateral surface of a central sterile disc, or over the entire surface of a dome-shaped ectostroma.

Melanconis stilbostoma (Fr.) Tul. is in many respects similar to the last-mentioned. Its ascospores are hyaline, not appendaged, and sub-biseriate in the ascus. The disc is whitish or yellowish, and the elliptical to ovate conidia are definitely brownish and are accompanied by smaller, rod-shaped, hyaline conidia, according to the figures of the Tulasnes (123, Pl. 14, fig. 4).

M. chrysostroma (Fr.) Tul., which is apparently the same as *Diaporthe sulphurea* Fck. and *D. decipiens* Sacc.,⁵ has 2-celled hyaline to yellowish ascospores with an obscure apiculus at each end. The spores are biseriate

⁵ The exsiccatum of *M. chrysostroma* given out by Ellis (N. A. F. 2d ser., no. 1563) and checked by Winter, is merely an old, over-mature specimen of *D. decipiens* Fck., which Ellis (29, p. 527) says is doubtfully distinct from *D. sulphurea* Fck. Both Winter and Ellis are in doubt as to there being any difference between *D. sulphurea* and *M. chrysostroma*. Petrak (91, p. 292) also remarks upon the similarity of these two species.

in an elongate-clavate ascus. The disc is here distinctly yellowish-green. The Tulasnes figure elliptical to cylindrical, one-celled, hyaline conidia, and also ovate-pyriform brown conidia (123, Pl. XXIV, figs. 14-17). Von Höhnelt (54, p. 198) reports large oval spores in the imperfect stroma (*Discosporium deplanatum* (Lib.) v. H.) of *M. chrysostroma*. These he considers as young conidia of the *Melanconium bicolor* β *ramulorum* Cda. pictured by the Tulasnes. Petrak (91, p. 293) disputes this connection on purely theoretical grounds. These connections are by observation only, and should be checked by culture work.

Melanconis juglandis (E. & E.) Graves has hyaline to light-grayish-olive ascospores, which are arranged in an obliquely uniseriate manner in the ascus. This species has a yellowish conical disc. Graves (38) has obtained the oval olive-gray conidia of *Melanconium oblongum* Berk. in his cultures of this fungus. Only spores of this type are found in the pustules in nature. In culture, however, Graves obtained also pycnidia containing small oblong, hyaline conidia.

The spores of *Melanconis Decoraensis* Ell. are 2-celled, brown, and arranged uniseriately in a long-cylindrical ascus. This species has a small yellowish-green disc, and was found by Ellis to be accompanied by a *Melanconium*. The writer has also found a *Melanconium* associated with this species (*Mycologia* 18: 263).

Melanconis spodiæa Tul., which according to Ellis differs from the preceding species only in its appendaged spores, is described by Winter as having a yellow-green disc and brown ascospores, arranged uniseriately to biseriately in a cylindrical ascus. The Tulasnes (123, Pl. XXIV, figs. 12, 13) figure both ovate brown and cylindrical hyaline conidia for this species also.

Two species should be mentioned here which are apparently exceptions to the general structure of this group. Both of these species, *Diaporthe galericulata* (Tul.) Sacc. and *D. albovelata* (B. & C.) Sacc., lack any marginal zone but show a well developed entostroma and a poorly defined ectostroma. *D. galericulata* was studied in culture by the writer (129), but produced no conidial fruit bodies. A *Fusicoccum* with hyaline conidia is reported as belonging to this species. This connection is only by association, and may prove to be incorrect. *D. albovelata*, in the writer's (127) cultures on sterile twigs of *Tilia americana* L., formed a sporodochia type of imperfect stage (*Sporocybe Rhois* (B. & C.) Sacc.) with one-celled colored spores. There were formed, however, on both agar and twig cultures, all transitional forms between the long-cylindrical fruit bodies of *Sporocybe* and loosely stromatic structures of a pulvinate shape, within which similar spores were formed. Pycnidial cavities containing one-celled, hyaline, fusoid-elliptical conidia were also found above the perithecial stromata. This may be considered as a species with a specially developed imperfect stage.

The preceding species, although they have been placed arbitrarily in

either the genus *Diaporthe* or the genus *Melanconis*, show a close relationship in the presence of a well defined, often colored, ectostromatic disc; in the absence of any recognizable entostroma; and in the possession of a *Melanconium* stage in their life history. The two species *D. galericulata* and *D. albovelata* are somewhat doubtful in their relationships and must await further study of other species of this group for a determination of their true position. In addition to these related forms, there remain certain species that have been placed in the genus *Melanconis* whose relationships seem to lie with the genus *Pseudovalsa* and which will be discussed under that genus.

Pseudovalsa

The genus *Pseudovalsa* is usually distinguished from *Melanconis* by its many-celled ascospores and by the possession of a *Coryneum* or *Stilbospora* stage in the life history. In the following discussion certain species of *Diaporthe* and *Melanconis* with a similar stromatic development and septate conidia will also be considered. Cultural life histories are badly needed to supplement the incomplete, and in many cases unreliable, knowledge of the imperfect stages of this group. The conidial stages of these species so far reported seem to point to a very interesting development of the forms now placed in *Pseudovalsa*.

The imperfect stages of this group have one type of conidium which is either hyaline or colored and septate, and usually a second type in the same species which is short, rod-shaped, more or less curved, hyaline, and one-celled. The hymenial cavities of the conidial stromata are more variable in these than in the *Melanconium* forms. These cavities may be either on the flanks of a central sterile disc, more or less sunken in the surface of the dome-shaped surface of the ectostroma, or may be entirely enclosed so as to form locules within the stroma.

We have previously noted the occurrence of both two-celled, hyaline, crescent-shaped, and one-celled, hyaline, rod-shaped conidia in *Gnomonia leptostyla* (Fr.) Ces. & de Not. Although the evidence as to the origin of these forms with septate conidia is unsatisfactory and fragmentary, this species presents an interesting possibility as an ancestral form of the group.

For the first examples of species of this type in the genus *Diaporthe*, let us examine the segregated genus *Cryptodiaporthe* of Petrak (89, p. 117). Petrak erected this genus for certain species of *Diaporthe* which show little or no development of entostromatic mycelium about the perithecia, which in turn are rather loosely aggregated. In this group he has included *D. aesculi* (Fck.) v. H., *D. Hystrix* (Fck.) Sacc., *D. spina* Fck., and *D. salicella* Sacc. Petrak found *Septomyxa aesculi* Sacc., with 2-celled conidia, associated with *D. aesculi*, and therefore supposes that this group is characterized by a *Septomyxa* stage. He transfers *Discella carbonacea* (Fr.) Berk. & Br., which he previously published as the imperfect stage of *Diaporthe tessella*, to *D. salicella* upon this supposition. The species of *Septomyxa*, he points

out correctly, are merely variations of *Discella* forms with more open hymenial cavities. These connections, to be sure, are by association only and some of them smack strongly of the personal equation, but they are very suggestive nevertheless, and if such connections can be substantiated by cultural studies they will show the origin of septate conidia among the lower forms.

Diaporthe furfuracea (Fr.) Sacc., which was carried in culture by the writer (127), is interesting in this connection. In culture, this species produced long, fusoid-cylindrical, hyaline conidia with 1-3 very faint septa. These septa are nearly obscured by the numerous oil drops present, but can be brought out by treating the spores with a solution of phenol in xylol. In agar the conidia were abnormally bent or twisted, but showed a definite central septum. These spores were whitish in mass. A second type⁶ of short, hyaline, one-celled, rod-shaped conidia was also formed, which were greenish-black in mass. In many cases the conidia were formed in enclosed locules beneath the surface hymenial cavities, as well as in these surface layers. This species does not agree entirely with the above-described group, since there is often present a thin but distinct darkened zone about the perithecial clusters. We shall see as we proceed, however, that there are other species of both *Melanconis* and *Pseudovalsa* which show a faint darkened zone. This species was carried in culture for two years before conidia of the rod-shaped type were produced, and then only sparsely on the terminal portions of sterile twigs. This is interesting evidence for the view that all the species of *Diaporthe*, *Melanconis*, and *Pseudovalsa* possess the potentiality of producing two types of conidia. Where one of these types is not known, we may consider that it is merely suppressed and would appear under the proper conditions.

Certain species which have been placed in the genus *Melanconis*, but which lack a definite ectostromatic disc, provide us with the next step in the development of this series.

Melanconis occulta (Fck.) Sacc.⁷ has perithecia in clusters of 2-4, and a disc composed of the fused and enlarged perithecial necks. The ascospores are large ($38-45 \times 13-15 \mu$), and have a broad, hyaline, recurved appendage at each end. The asci are broadly clavate, and the spores are biserially arranged. There seems to be no authentic connection of an imperfect form. *M. Everhartii* Ell. is very similar to the last-named species, having a disc composed merely of the thickened perithecial necks. The ascospores are

⁶ Both types of these conidia have since been found in nature on *Tilia americana*, in association with *D. furfuracea*.

⁷ This species has been placed in the genus *Diaporthe* by von Höhnelt (57, p. 387) on the basis of the absence of paraphyses. Petrak has reported the absence of paraphyses from *M. spodiacea* and *M. appendiculata*, and erected the sub-family "Pseudodiaportheen" for the dark-spored species of *Melanconis* (*Melanconiella*) without paraphyses. The presence and absence of paraphyses has been proved or disproved for nearly every species of *Melanconis*, and this is a very unreliable character, especially when determinations are made from dried herbarium material.

large ($25-38 \times 8-11 \mu$), have a broad, curved appendage at each end, and are arranged biseriately in a broad, clavate ascus. The writer knows of no conidial connection for this species.

In the case of *M. thelebola* (Fr.) Sacc., we have an interesting transition. In this species, as in *Diaporthe furfuracea*, we often find a faint, dark, marginal line. The ascospores are large, hyaline, usually 2-celled, and with a long setaceous appendage at each end. The writer has seen these ascospores with 2-3 septa when fully mature. There is often a development of stromatic mycelium about the perithecial necks, but this is chiefly entostromatic. The Tulasnes (123, Pl. XXI, figs. 3-12) figure enclosed locules within this stroma, in which are formed two types of conidia.⁸ One type is a short, curved, rod-shaped, one-celled, hyaline conidium, the other is larger, clavate, brown, and 3-septate. We have here a species with 2-celled hyaline ascospores (which may become 2- to 3-septate), which shows the typical brown, pluriseptate conidia of the genus *Pseudovalsa*. The formation of these conidia within a locule, which occurs in this species, is a variation that, as we have seen, is common in the lower forms of this group.

In *Melanconis modonia* Tul. the bark tissues above and about the perithecia are rather heavily blackened and interspersed with entostromatic mycelium. The ascospores are large ($27-35 \times 10-11 \mu$), irregularly biseriate in the ascus, and according to the descriptions become light brown at maturity. Petrak (94, p. 323) recognizes this species as transitional between *Melanconis* and *Pseudovalsa*. He reports that the ascospores become 2- to 3-septate at maturity, and upon this fact and the character of the stroma places it in *Pseudovalsa*. This species has a Coryneum with 3- to 8-septate brown spores for its imperfect stage. This imperfect stage with the conidia borne on the surface of the stroma is characteristic of the genus *Pseudovalsa*. The Tulasnes (123, Pl. XV, figs. 1-5) show this spore form and also a second, consisting of small, rod-shaped to allantoid, hyaline, one-celled conidia, formed in open cavities on the sides of a central sterile disc.

The preceding species of *Diaporthe* and *Melanconis* are similar in the presence of septate conidia borne in shallow cavities or in more or less enclosed locules within a stroma. There is a general lack of a sharply defined ectostroma. We can note a general tendency towards the septation and coloration of both the ascospores and the conidia of one type. The ascospores become large, but remain biseriate in the ascus; they also become appendaged in many species, but this is not a distinctive character, since it also occurs in the other two groups.

The species of *Pseudovalsa* show a continuation of the development traced in the preceding species. The ascospores of the genus *Calosporella*,

⁸ Von Höhnelt has erected the genus *Pseudovalsella* for this species on account of the conidial connections. He designates the pycnidia with rod-shaped conidia as *Cytosporopsis umbrinus* (Bon.) v. H., and the pycnidia with the brown septate conidia as *Hendersoniopsis thelebola* (Sacc.) v. H., in spite of the fact that the Tulasnes picture both types of conidia in the same locule.

which are 4-celled and hyaline, have been variously interpreted as 4-celled Diaporthe spores or hyaline Pseudovalsa spores, which fact shows that they are merely transitional species. The spores of many species of Pseudovalsa remain hyaline until almost mature. Petrak (94, p. 323) points out that *P. aucta* (Berk. & Br.) Sacc. is a transitional species between *Melanconis* and *Pseudovalsa*, since the ascospores remain 2-celled and hyaline for some time.

Petrak (94, p. 323) divides the genus *Pseudovalsa* into two genera. He places in the genus *Prosthecium* Fres. those species which develop little or no entostromatic mycelium, have few paraphyses, and possess appendiculate ascospores. These species, it can be seen from these characters, are closely related to the forms of *Melanconis* discussed under this genus. In the genus *Pseudovalsa*, Petrak retains those species with a well developed entostroma in which the perithecia are usually developed. The ascospores in these forms do not possess appendages. These species have a faint darkened marginal zone, as we have noted for *Diaporthe furfuracea*, *Melanconis modonia*, and *M. thelebola*, and may be considered the climax type of this series.

Many species of *Pseudovalsa*, as *P. lanciformis* (Fr.) Ces. & de Not., *P. umbonata* (Tul.) Sacc., *P. longipes* (Tul.) Sacc., *P. Berkeleyi* Sacc., *P. stilbospora* Auers., and *P. sigmoidea* (Cke. & Ell.) Sacc., have been reported as having either a Coryneum or a Stilbospora type of imperfect stage; which means that the elongated, many-celled, brown conidia are borne upon the surface of an ectostromatic cushion, which may or may not be erumpent through the periderm. This represents the ultimate development of the more or less chambered fruit bodies with hyaline or brown, septate conidia, found in the forms previously discussed. A second type of short, rod-shaped, more or less curved, hyaline, one-celled conidium is also reported for some species of this genus. Such conidia are figured by the Tulasnes for *P. umbonata* (123, Pl. XV, fig. 9) and *P. lanciformis* (Pl. XVI, figs. 9-11). Von Höhnelt (51, p. 683) reports that a *Cytospora* (*Dothiorella*?) belongs to *P. Berkeleyi*.

The writer (*Mycologia* 18:264) has had only one *Pseudovalsa* (*P. longipes* (Tul.) Sacc.) in culture. This species produced a Coryneum stage on *Tilia*, and, although it produced the second type of filiform hyaline conidia, this occurred only on sterile twigs of *Quercus*. These conidia are borne on the irregular exposed surface of a black, erumpent ectostroma, composed of erect septate hyphae. This species again illustrates the formation of the two types of conidia under different environmental conditions; in this case it was a difference of host substrata.⁹

Summary (First Series)

In conclusion let us summarize the main phylogenetic outlines of this series. In the first place, we have traced the origin of the series from

⁹ Since this was written the filiform type of conidium has been obtained upon twigs of *Tilia* which were coated with paraffin before being inoculated.

species similar to those of the genus *Gnomonia*. The genus *Diaporthe*, as it has been limited in this discussion, consists of a compact group in which the formation of an entostroma has taken place early in the evolutionary development of the genus. The strong development of a hyaline entostroma has produced in these species a light-colored, differentiated entostromatic area, circumscribed by a dark marginal zone. The imperfect stage of these forms consists of a *Phomopsis* type of fruit body, with an enclosed locule formed in an ectostroma which is intimately associated with the entostroma beneath, when that tissue is well developed. The conidia are of two types, both one-celled and hyaline. The ascospores in this group remain hyaline, 2-celled, and biseriate in the ascus, but may become appendaged in some forms. The paraphyses are delicate, and very few remain in the mature perithecium.

Developing parallel to this *Diaporthe* group we find a second series which does not produce a dark marginal zone, at least until late in the history of its development. This series in turn shows two sub-divisions.

In the first of these sub-divisions (*Melanconis*) the stromatic development is limited to an ectostromatic disc, and the perithecia are imbedded in the unaltered cortex. The ascospores of this series, which culminates in the genus *Melanconis* (*Melanconiella*), become colored and uniseriate in the ascus in the higher forms, but remain 2-celled. The paraphyses become more numerous in this group than in *Diaporthe*, but are still evanescent. The imperfect stage is typically a *Melanconium*, with the conidia borne in shallow cavities on the sides of a sterile disc, or over the entire surface of a dome-shaped ectostroma. The conidia are of two types. One type is elliptical to ovate, one-celled, and more or less dark-colored; the second type is smaller, oblong to rod-shaped, one-celled, and hyaline. In some of the higher forms of the group, the second type is suppressed and occurs only rarely.

In the second sub-division of this second group there is no definite ectostroma, and, where a stromatic mycelium is formed, it is within the bark about the perithecial necks and the perithecia. The origin of this group is doubtful, and further cultural studies of the lower forms are needed. Where a development of an entostroma takes place a faint dark marginal zone appears, but the entostromatic mycelium is usually dark-colored and the stromatic areas are not light-colored, as in *Diaporthe*. The ascospores become dark-colored, and in the higher forms 2- to many-septate. The ascospores of a number of species are appendiculate. The paraphyses show a higher development in this series, and become very numerous in some of the higher forms.

The imperfect stage of this *Pseudovalsa* group is ectostromatic, but these ectostromata are usually not connected with the perithecial stroma, or where they are, as in some species of *Pseudovalsa*, they are reduced. The imperfect fruit body consists of either shallow cavities on the sides of a

sterile disc, a more or less open layer over the entire dome-shaped surface of the ectostroma, or enclosed locules within the ectostroma. Two types of conidia are formed. One type consists of elongate-elliptical to clavate, one- to many-septate, hyaline or brown spores. The second type consists of smaller, rod-shaped, curved, one-celled, hyaline conidia, which are borne in the same cavity as the first type or in separate cavities or even in separate stromata.

If space permitted, the writer would like to discuss in detail the confusion that has arisen as a result of the fragmentary considerations of the three genera just discussed. The separation of these genera has been necessarily vague, since they are integral parts of the same developmental series. They have been separated on groups of characters, such as spore-color and septation, presence or absence of paraphyses, and type of imperfect fruit body, all of which vary independently.

Time and again, the European mycologists working upon this group have transferred species or erected new genera on a consideration of only one or another of these varying characters, or by a consideration of only one or a few species, without any regard to the general relationships within the group. As a result, we have a large number of genera, as *Diaporthe*, *Melanconis*, *Melanconiella*, *Cryptodiaporthe*, *Allantoporthes*, *Apioporthes*, *Discodiaporthe*, *Calospora*, *Calosporella*, *Pseudovalsellula*, *Prosthemium*, *Pseudovalsa*, *Aglaospora*, and many others, whose limits are vague and overlapping, and all of which have been delimited from closely related groups of species. If these workers would not insist on creating and tearing down genera on fragmentary considerations of one or a few species, and on frequently incorrect observational inferences concerning the connection of the imperfect stage, but would instead stop to determine definitely by cultural methods the questions presented, we should advance more rapidly to an understanding of the true relationships existing between genera instead of remaining constantly entangled in the confusion of contradictory synonymies.

From the implications that might be derived from the preceding facts, it may be suggested, in a tentative way, that the only genera with sufficiently valid background are those which represent a developmental series, or an integral portion of such a series, such as the three groups we have just outlined.

Second Series

Under this second series we shall consider certain genera with one-celled ascospores. The main line of development in this group (*Cryptosporella* and *Cryptospora*) shows a similar stromatic structure and a similar imperfect stage. The relationships among the lower forms of the series are still rather vague. The genera *Gnomoniella*, *Mamianiella*, *Diaporthopsis*, and *Mazzantia* all probably represent small groups with a special development of the stroma. *Gnomoniella* has no stromatic development, and may be

considered as the ancestral form. *Sphaerognomonia* shows the development of a stromatic "clypeus" about the ostiole, while *Mamianiella* shows a well developed stroma about the perithecium. These three genera are leaf-inhabiting. The genus *Mazzantia*, as von Höhnelt (60, p. 109) points out, has a stromatic structure identical with that of a well developed *Diaporthe*, but has one-celled ascospores. *M. galii* (Fr.) Mont. shows a strongly developed, differentiated entostroma within the tissue of the substratum, which is bounded by a darkened zone. Von Höhnelt has erected the form genus *Mazzantiella* for the imperfect forms of *Mazzantia*. In these fruit bodies an enclosed locule is formed within the stroma. The conidia are cylindrical and hyaline.

The writer has not examined any species of the genus *Diaporthopsis*, but, judging from descriptions, they form a more or less effused entostroma which is often bounded by a faintly darkened zone. Diedicke gives a *Phomopsis* as the imperfect stage of *Diaporthe* (*Diaporthopsis*) *nigrella* (Auers.) Niessl. Von Höhnelt (60, p. 114) considers this genus as closely related to the subgenus *Euporthe*, or more likely to the *Hyponectriaceae*.

Whether or not some species of *Diaporthe* may have arisen from such forms with one-celled ascospores and rather well developed stromata, is a question which can not be answered at present. It is true that some species of *Diaporthe* show ascospores which are tardily or very faintly septate. Some such species have been described under the genus *Cryptosporella*. On the other hand, there are numerous species of *Diaporthe* with very simple stromatic structure which nevertheless show definitely septate ascospores.

Cryptosporella and Cryptospora

Cryptosporella and *Cryptospora* are the characteristic genera of this series. Von Höhnelt (60, p. 106) noted the "euvalloid" character of the perithecial centrum in these two genera, and placed them in his "*Diaportheen*."

The species of both *Cryptosporella* and *Cryptospora* are characterized by a sharply defined conical ectostromatic disc, about which the perithecia are arranged circinately within the unaltered bark cortex. There is no differentiated entostromatic area nor dark marginal zone. The imperfect stages of these two genera have been placed in the form genera *Fusicoccum* and *Disculina* (*Cryptosporium*). The structure of these fruit bodies is very similar to that of those found in the first series. They consist of an ectostromatic cushion which contains open cavities or enclosed locules, usually on the marginal portions of the ectostroma. The conidia are one-celled, hyaline, and usually more or less elongated.

The characters just mentioned show a relationship between these two genera and those species which were discussed under the genus *Melanconis*. The chief differences are the non-septate ascospores and the hyaline, usually elongated conidia. In some species of *Cryptospora* (*Sillia*) the ascospores

become septate, but the long-cylindrical shape easily distinguishes these spores.

According to von Höhnelt (60, p. 106), *Cryptosporella populina* (Fck.) Sacc. has a faint septum in its ascospores, and is the same as *Diaporthe populea* Sacc. Von Höhnelt gives a Phomopsis as the imperfect stage of this fungus. He also gives a Phomopsis as the imperfect stage of *C. Niesslii* (Kze.) Sacc., which has one-celled ascospores and which he considers as synonymous with *Diaporthe hystrix* (Tode) Sacc. An examination of this species (Syd. Myc. Germ. no. 2135) by the writer has shown that it has a stromatic structure typical of *Cryptosporella*, with a well developed ectostroma surrounded by the circinate perithecia in the unaltered bark cortex. Associated with these stromata, furthermore, was found an imperfect stage consisting of ectostromatic cushions with shallow, more or less exposed cavities on their sloping sides. These cavities contained one-celled, hyaline, elliptical to cylindrical conidia $6.5-13 \times 2.5 \mu$. These cavities may sometimes be formed more deeply within the stroma, and then resemble a Phomopsis, but the structure is typically that of a *Cryptosporella*. As we have previously seen, Petrak has placed both *Diaporthe hystrix* and *D. populea* in his genus *Cryptodiaporthe*, which is supposed to have *Septomyxa* as its conidial stage. All of which merely shows the necessity for cultural connections and for a clearer conception of the form genera concerned.

Other species have been placed here, as for example *Cryptospora pennsylvanica* (B. & C.) Ell., *C. aculeans* (Schw.) Ell., and *Cryptosporella anomala* (Pk.) Sacc., whose relationships are not with this group, but the important point is that the true *Cryptosporellas* show a correlation of characters. They have one-celled, elliptical to fusoid ascospores, the stromatic characters previously described, and an imperfect stage consisting of one-celled, hyaline, elliptical to fusoid conidia formed in more or less open cavities or locules in the surface of an ectostroma. Von Höhnelt (60, p. 106) gives the imperfect stage of *C. Daldiniana* as *Fusicoccum Lesourdianum* Sacc. & R., and that of *C. aurea* as *F. amygdalinum* (Sacc.) v. H.

The genus *Cryptospora* is similar in all respects to *Cryptosporella*, except that the ascospores are long-cylindrical instead of elliptical or fusoid. The stromatic characters are the same. The imperfect stage is very similar, except that the conidial hymenium is usually more exposed, and the conidia are long-cylindrical and slightly curved instead of fusoid-elliptical. This type of fruit body falls in the form genus *Cryptosporium* Sacc. or *Disculina* v. H. The Tulasnes (123, Pl. XVII, figs. 13, 15, 28-30) figure such imperfect stages for *C. suffusa* (Fr.) Tul. (*Disculina Neesii* (Cda.) v. H.), and for *C. betulae* Tul. (*Disculina betulina* (Sacc.) v. H.). The Tulasnes (123, p. 175) reported spermagonia with hyaline allantoid conidia $13 \times 2.5 \mu$ associated with *C. corylina*. Von Höhnelt (60, p. 108) reports a *Disculina* (*D. corylina* v. H.) associated with this species also. According to Allescher (2, p. 745), Fuckel reports similar small, cylindrical, hyaline conidia in the hymenial

layer of *Fusicoccum amygdalinum*, the imperfect stage of *Cryptosporella aurea*.

The writer has had two species of *Cryptospora* in culture (unpublished). *C. (Sillia) cinctula* (Cke. & Pk.) Sacc. failed to fruit either on agar or on sterile twigs of *Castanea*. Cultures from a specimen of *C. suffusa* (Fr.) Tul. on *Hamamelis virginiana* L. formed a conidial stage on sterile twigs of *Hamamelis*. A pulvinate ectostroma was formed, composed of parallel septate, greenish-black hyphae. On the lateral portions of this ectostroma locules were formed, which soon opened to the exterior, forming shallow cavities. The conidia produced in these cavities were oblong-cylindrical, one-celled, hyaline, and $9-13 \times 2.5 \mu$. This formation of small cylindrical conidia in culture, together with the two cases already mentioned in which such conidia were found in connection with *Cryptospora* and *Cryptosporella*, shows that the species of this series may also produce two types of conidia, and completes the resemblance of this series to the one previously discussed.

Von Höhnelt (60, p. 108) has placed certain species of *Cryptospora* which show one or more cross walls in their ascospores in the genus *Sillia*. The writer knows of no conidial connection with any of these species.

In conclusion, we see that this second series of the *Diaporthaceae* differs from the first chiefly in the non-septate character of the ascospores (becoming faintly septate in some species of *Cryptospora*), and in the non-septate, hyaline character of the conidia. The presence of a sharply defined ectostroma, the lack of either an entostroma or a darkened zone, and the non-septate conidia place them in closest relation with the species previously discussed under the genus *Melanconis*.

The lower forms, as we have seen, present several small specialized groups with more or less well developed stromata. *Cryptosporella* and *Cryptospora* show a short line of development, with a tendency towards the elongation and septation of the ascospores and a similar elongation of the conidia. *Mazzantia*, *Cryptospora*, and *Cryptosporella* all seem to be valid genera of this series.

Third Series

The third series of related forms within the *Diaporthaceae* includes the genera *Valsa*, *Leucostoma*, *Valsella*, *Endothia*, and *Valsaria*. *Leucostoma* will here be considered as a separate genus on account of its distinctive stromatic development. Von Höhnelt (60, p. 130) separates *Leucostoma* as a genus on the basis of the white disc, the long perithecial necks, and the well developed entostroma. Petrak (89, p. 128) rightly points out that the first two characters do not distinguish *Leucostoma* from *Euvalsa*. He discards the stromatic character as a differentiating one because, as he says, certain species of *Euvalsa* have this character. This stromatic development is, however, the differential character, and if these species (which he does not mention) possess such stromatic characters they belong in *Leucostoma* and not in *Euvalsa*.

Von Höhnelt (60, p. 130) places *Valsa*, *Leucostoma*, and *Valsella* in the "Valseen," a separate sub-family of his "Diaportheen," in contrast to his "Eu-Diaportheen" in which he includes all the genera discussed in the first two series. This seems to the writer a logical separation on the basis of general relationships. We have seen in the previous discussion that both the perfect and the imperfect stages of the first two series are very similar in structure, the difference between the two series being mainly one of spore characters.

In this third series, however, we find quite marked differences in both stages of the life history from the species of the first two series. In *Euvalsa* the structure is quite simple and resembles that of *Melanconis*, but in the other genera there is a well developed and strongly differentiated entostroma. The ascospores of all the species of this series, except some species of *Endothia* and *Valsaria*, are, moreover, allantoid, hyaline, and one-celled. The imperfect stage also is here quite different. The conidial chambers in this series are numerous or labyrinthiform, and are produced not only in the ectostromatic but also in the entostromatic tissues. The conidia are small, one-celled, hyaline, and cylindrical to allantoid.

The genus *Glomerella*, with its allantoid ascospores, presents a possible origin for this series among the simple *Sphaeriales*. There seems to be, however, a rather wide gap between such forms and the species of *Valsa*.

Valsa

Valsa is a large, but distinct and compact genus. In the older classifications it was usually placed with the genera here placed in the *Allantosphæriaceae*. It differs from these genera in the character of its perithecial centrum, its hyaline ascospores, non-stipitate asci, non-sulcate ostioles, the lack of any dark marginal zone, and in the character of its imperfect stage; there remains only a very superficial resemblance.

The species of this genus have a definitely differentiated truncate-conical ectostroma, which forms the erumpent disc. The perithecia are buried in the bark cortex beneath this ectostroma. There may be a slight development of entostromatic mycelium about the perithecia, but there is no differentiated area, and even under a hand-lens the perithecia appear to be imbedded in the unaltered bark cortex. Ruhland (99), in his discussion of *Valsa salicina* (Pers.) Fr., contradicts himself in regard to the character of the ectostroma. On page 52 he says: "Wie überhaupt bei den Arten der Subgenera *Leucostoma* und *Euvalsa* ist auch hier die Grenze zwischen Ecto- und Entostroma auf ausgebildeten Stadien keine scharfe." Later, on page 54, he says for the same species: "Das Ectostroma, welches stets gut von dem mycelartigen Entostroma abgesetzt ist" The entostroma of this species is visible only under the microscope, while the ectostroma is very sharply defined.

The imperfect stage of the genus *Valsa* is very constant, belonging to

the form genus *Cytospora*. The fruit bodies consist of a stromatic tissue in which there are formed numerous locules, which often coalesce to form a labyrinthiform chamber. The conidia are small, allantoid, one-celled, hyaline, and ejected in large numbers in the form of a spore horn. In both *Valsa* and *Leucostoma* the pycnidial locules arise in the same tissue as the perithecia, but the two types of fruit bodies are practically never found in the same stroma. The pycnidial locules of the species of the genus *Valsa* arise in mats of entostromatic mycelium which are formed within the bark tissues. These entostromatic masses of mycelium are not very extensive, and there is comparatively little stromatic tissue remaining about the locules at maturity. The result is a thin-walled labyrinthiform pycnidium imbedded in the cortex, which is characteristic of this genus.

Leucostoma

The stromatic development of the species of the genus *Leucostoma* is quite different from that of species of the genus *Valsa*. As Ruhland (99) has pointed out in his discussion of *V. (Leucostoma) nivea* (Pers.) Fr. and *V. (Leucostoma) superficialis* Nit., the differentiation between ectostroma and entostroma is very vague in this genus. In some species, as *V. (Leucostoma) subclypeata* Cke. & Pk., there is formed a differentiated cap of ectostromatic mycelium, but in many species this is very poorly developed and scarcely distinguishable. In all the species of this genus the stromatic area is delimited very early in its development by a dark marginal zone of tissue, which limits the size of the stroma. The position of this delimiting zone varies in the different species. In *V. (Leucostoma) leucostoma* (Pers.) Fr. this zone runs just beneath the periderm, and the stroma develops between the periderm and the bark surface. In other cases, as *V. (Leucostoma) nivea*, *V. (Leucostoma) translucens* (de Not.) Ces. & de Not., and *V. (Leucostoma) superficialis*, this zone may penetrate into the bark to a depth of 3 to 5 layers of cells. The perithecia may then develop either in or on the surface layers of the bark. In *V. (Leucostoma) subclypeata* this blackened zone penetrates deeply into the bark, cutting off a spherical area within which the bark cells are absorbed and replaced by a stromatic fungous tissue. In all the preceding cases there is a strong development of stromatic mycelium about the perithecia, so that the mature stroma is composed almost entirely of fungous tissue, with only a few disintegrated remains of the bark cells. It can be seen that the terms ecto- and entostroma, as defined at the beginning of this discussion, apparently break down here. Where there is a differentiated cap of tissue formed which functions in the opening of the periderm, the stromatic tissue in which the perithecia are imbedded should undoubtedly be considered as entostroma. In many cases, however, this tissue develops entirely upon the bark surface. Where it does arise in the surface bark layers, these are soon absorbed or imbedded in the fungous tissue. Even where the darkened zone penetrates into the

layers of bark cells, these cells often remain comparatively intact and the perithecial stroma develops above them. Ruhland (99) considers this tissue in which the perithecia are imbedded as entostroma, and this is probably the correct interpretation, since many species show a differentiated ectostroma above it.

The pycnidial locules of this genus, which are numerous or labyrinthiform, are produced in a stroma identical with that in which the perithecia are formed, except that in some cases the tissues of the pycnidial stroma become blackened and so obscure the bounding zone. The pycnidia of the species of *Leucostoma* show a greater stromatic development than those of the genus *Valsa*, corresponding to such a development in the perithecial stromata. Von Höhnelt (60, p. 130) has erected the form genus *Leuco-cytospora* for this more stromatic type of *Cytospora* fruit body.

Valsella

The genus *Valsella* differs from *Leucostoma* only in its polysporous asci. As has previously been noted under the discussion of the polysporous Allantosphaeriaceae, Petrak (94, p. 227) considers the species of *Valsella* as not distinct from certain corresponding species of *Leucostoma*, but merely polysporous forms of these produced under certain conditions. Although Sydow's Myc. Germ. no. 2132 of *V. (Leucostoma) translucens*, distributed as an example of the association of such 8-spored and polyspored forms, seems to bear out this view, its validity can be determined finally only by cultural proof. The writer (128) has obtained perithecia of *V. (Leucostoma) Kunzei* Fr. in culture, but has not as yet observed the occurrence of any polysporous asci.

The imperfect stage of the genus *Valsella* is the same as that found in *Leucostoma*.

Endothia

Von Höhnelt places the genus *Endothia* in his "Diaportheen" on the basis of the structure of the perithecial centrum. This genus was excluded from his "Valseen," apparently because that subfamily includes only allantoid-spored forms. Both *Endothia gyrosa* (Schw.) Fr. and *E. singularis* (H. & P. Sydow) S. & S., however, have long-elliptical to allantoid, one-celled or pseudo-septate ascospores, and this fact, together with the formation of stromatic pycnidia containing labyrinthiform locules, suggests to the writer that the position of this genus is close to that of *Leucostoma*.

The development of the stroma in *Endothia* is variable and often difficult of interpretation. In *E. parasitica* (Murr.) P. J. & H. W. And., as pointed out by P. J. Anderson (3), the stroma usually originates as a hyaline ectostromatic cushion just beneath the periderm. The amount of this tissue formed varies widely. If a sufficiently well developed ectostroma is produced, pycnidial locules are formed within it. If this tissue is much reduced it remains sterile, and unless pycnidial locules are formed within the

entostroma, which may also occur, there results a stroma with perithecia only. About the time the ectostroma ruptures the periderm its tissues become tinted a yellow, and finally a reddish-orange color. The perithecial initials are formed within the bark cortex beneath the ectostroma. Along with the development of the perithecia there is a formation of entostromatic mycelium. This entostromatic development is often very vigorous, and a large stromatic mass containing only the remnants of the bark cells is pushed up through the periderm. Wherever the stroma becomes exposed in this manner it undergoes the characteristic coloration. In these larger stromata the ectostroma can no longer be distinguished. In a less well developed stroma it can often be seen, however, as a conical orange-colored disc. Shear's (110, p. 26) statement that the stroma of *E. parasitica* can not be divided into ecto- and entostroma seems to be based upon the supposition that these terms are synonymous with conidio- and ascostroma. Many of his figures show the differentiation of two types of tissue. In his Plate XV, figure 2, he shows two sterile ectostromata; figure 1 shows an ectostroma with a pycnidial locule forming in its base; and figure 3 shows pycnidial locules forming within the entostroma. Plate XIV, figure 2 of the same bulletin shows a sterile ectostroma with both a perithecium and a pycnidial locule forming in the entostroma beneath, while Plate X, figure 1 shows a slightly developed ectostroma with the perithecia beneath in the entostroma.

Such species as *E. gyrosa* and *E. singularis* show an exceptional growth of entostroma, resulting in a large crumbly mass of fungous tissue in which only the remnants of the bark cells can be found. This type of entostromatic development is similar to that already noted in the genus *Valsaria*.

In this genus the entostromatic development is not limited by the formation of a blackened limiting zone, as in *Leucostoma*, and the stromata become large and irregular in shape. The coloration of the stromatic tissues, the septation of the spores, and the cylindrical rather than allantoid conidia also separate it from *Valsa* and *Leucostoma*. The forms of this genus must have arisen therefore as a divergent line from some common ancestor of these other two genera.

Valsaria

The relationships of this genus and the reasons for placing certain species in the Allantosphaeriaceae have been discussed under that series. It remains here to show the similarities between such species as *V. insitiva* Ces. & de Not. and *V. exasperans* (Ger.) E. & E. and the preceding genera of this series.

These species of *Valsaria* differ from *Endothia* in the uniseriate, colored ascospores, the numerous paraphyses, and the total lack of any ectostromatic tissue. The structure of the ascus is, however, typical of the Diaporthaceae. The imperfect stage with its elliptical conidia formed within labyrinthiform locules is almost identical with that of *Endothia*, except that no ectostromatic

locules are formed. The coloration of the stroma, although black in *V. insitiva*, brown or mouse-gray in *V. exasperans*, and dull red in *V. rubricosa*, is also suggestive of the genus *Endothia*. The dark zone outlining the stroma, particularly in *V. exasperans*, is similar to that found in *Leucostoma*.

The preceding facts point to a common ancestral form for the genera *Leucostoma*, *Endothia*, and *Valsaria*. The dark-brown spores and the lack of any transitional forms, however, make the position of the genus *Valsaria* in this series only tentative.

This third series of the *Diaporthaceae* stands out in contrast to the other two series by virtue of its quite different imperfect stage. The genus *Valsa* presents the simplest forms. The genus *Leucostoma* differs only in the strongly developed entostromatic mycelium, which arises about the perithecia within a limiting blackened zone. The species of *Endothia*, arising probably from similar simple forms of a *Valsoid* type, have a different type of stromatic development and have developed a septate, elliptical ascospore. The genus *Valsaria* stands in a somewhat intermediate position, with the stromatic development of *Leucostoma* but with ascospores similar to *Endothia* but brown in color.

Summary (Diaporthaceae)

In the *Diaporthaceae*, as in the *Allantosphaeriaceae*, we have seen the development of the stroma taking place in several separate series of forms. These separate developmental series can be distinguished in this family by a constancy of certain correlated characters.

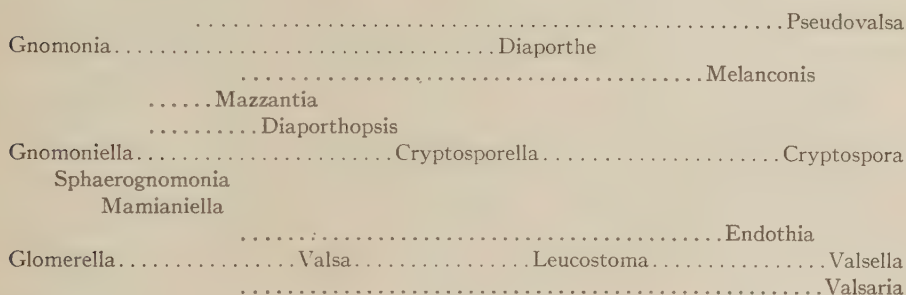
In the first series we have evidence of three diverging lines of development, made evident chiefly by differences in the septation and coloration of the conidia. The conidial fruit bodies are ectostromatic and bear their hymenium in enclosed locules, open cavities, or exposed layers. The conidia are of two types. One type remains cylindrical, one-celled, and hyaline throughout the series. The second type is one-celled and hyaline in *Diaporthe*, one-celled and colored in *Melanconis*, and hyaline or colored, but septate, in *Pseudovalsa*. The lower forms of these three diverging lines all have hyaline 2-celled ascospores, but the climax forms of each group show a distinctive type of ascospore. In *Diaporthe* the ascospores remain 2-celled and hyaline; in *Melanconis* they become 2-celled and brown; in *Pseudovalsa* they become many-celled and brown. Certain stromatic characters are also correlated with these differences in conidial characters and with the evolution of the ascospore, as already noted.

In the second series the ascospores are elliptical, hyaline, and one-celled to long-cylindrical, hyaline, and sometimes faintly septate. The imperfect fruit body is similar to that of the first series, but the conidia are all one-celled, hyaline, and somewhat elongated. A second type of conidium is present, at least in some species. The configuration of the perithecial stroma resembles that of *Melanconis*.

In the third series is found a set of characters which contrast it to both of the first two series. The ascospores are allantoid, one-celled, and hyaline to elliptical, 2-celled, and brown. The imperfect fruit body is either ectostromatic or entostromatic and consists of numerous labyrinthiform locules within a stroma. The conidia are small, allantoid to elliptical, one-celled, and hyaline. Only one type of conidium is known. The perithecial stromata are various in structure.

As the simple (non-stromatic) forms of the Diaporthaceae all have similar imperfect stages so far as known, the ancestral forms of these three series are suggested by the type of ascospore to be *Gnomonia*, *Gnomoniella*, and *Glomerella*, respectively.

The relationships of the Diaporthaceae may be represented diagrammatically as follows:



SUMMARY

From the preceding discussion we may draw the following conclusions:

1. It is no longer necessary to construct the taxonomy of the stromatic Sphaeriales upon purely arbitrary and uncorrelated characters; instead, one finds that there exist definite phylogenetically related groups which can serve as a basis for classification. It should be pointed out here that the stromatic Sphaeriales do not themselves form a complete line of evolution, but represent merely the higher stromatic development of lower forms. The Diaporthaceae and the Allantosphaeriaceae should include, therefore, in a natural classification, the simpler forms; as they are included in von Höhnelt's outline of these families. The stromatic forms were chosen merely as a convenient group for intensive study.

2. After determining these phylogenetic relationships, we can formulate certain generalities in regard to the evolution of the group as a whole, and, therefore, as to its classification:

(a) In the first place the evolution of the group has been polyphyletic, consisting of a number of parallel series. These series should comprise, therefore, the larger groups in any classification, according to their rank in the evolutionary series.

(b) The development of the stroma and the compound fruit body is

common to all the evolutionary series within this group. This character, therefore, can not be used as a differential character for the larger divisions of a taxonomic system. The minor variations of stromatic development are valuable, however, when used in correlation with other characters or to determine relationships within one given series.

(c) In this group at least, the characteristics of the imperfect fruit body are definitely correlated with those of the perfect stage, and are very valuable characters for the determination of relationships. The conidial fructification often shows an evolution parallel to that of the perithecial fructification, as is seen in the coloration of the conidia of the *Pseudovalsa* series or in the elongation of the conidia in the *Cryptosporella*-*Cryptospora* series. Characters of the conidial fruit body should not be used in the separation of taxonomic divisions, however, without the presence of correlated differences in the perithecial fruit body, on account of the practical difficulty of determining the genetic connection of the two stages of the life history.

With the preceding principles in mind, let us see what changes their application will make in the previous classifications in this group. For the sake of clarity, let us set down three taxonomic systems, which will illustrate the chief variations in viewpoint as to the classification of this group.

I. That of Lindau, in Engler and Prantl's "Natürliche Pflanzenfamilien" (1897):

Valsaceae:

Anthostoma	Vialaea	Caudospora	Rhyncostoma
Diaporthe	Kalmusia	Thyridella	Thyridium
Fenestella			

Valsa

Sub-genera:	Eutypa	Cryptovalsa	Leucostoma
	Endoxyla	Cryptosphaerella	Eutypella
	Cryptosphaeria	Endoxylina	Valsella
	Euvalsa		

Melanconidaceae:

Cryptosporella	Valsaria	Melanconis	Calospora	Pseudovalsa
Cryptospora	Titania	Melanconiella	Holstiella	

Diatrypaceae:

Calosphaeriae:		Diatrypeae:	
Calosphaeria	Cacosphaeria	Diatrype	Quaternaria
Coronophora		Scoptria	Pleurostoma
		Diatrypella	

Melogrammataceae:

Gibellia	Botryosphaeria	Myrmaecium	Melogramma
Endothia	Myrmaeciella	Sillia	Berlesiella

II. That of von Höhnelt (57, 59) given in 1918 (stromatic forms):

Allantosphaeriaceae:

Diatrypeen:

Cryptosphaeria
Quaternaria
Cryptovalsa
Diatrypella

Eutypa
Eutypella
Diatrype

Valseen:

Later transferred to the
Diaportheen.

Diaportheen:

Eu-Diaportheen:

Mazzantia Apioporthes
Diaporthopsis Endothia
Cryptosporella Diaporthe
Vialaea Calosporella
Cryptospora

Valseen:

Valsa (Scoptria and Pereneutypa,
Leucostoma related to Eutypella)
Valsella

III. A tentative grouping upon the basis of the preceding outline of the writer's conclusions:

Allantosphaeriaceae:

Diatrypeae:

Eutypa	Diatrype	Diatrypella	Eutypella	Cryptosphaeria Valsaria (<i>p.p.</i>) Anthostoma
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Diaporthaceae:

Eu-Diaportheae:

Diaporthe	Diaporthopsis
Melanconis	Mazzantia
Pseudovalsa	Cryptospora
	Cryptosporella

Valseae:

Valsa
Leucostoma
Valsella
Endothia
Valsaria (*p.p.*)

All the earlier systems of classification, from that of Nitschke (83) until the time of von Höhnelt's rearrangement of these genera, are modeled on a basis very similar to the system of Lindau given above. The four families used by all these workers are very indefinite and widely overlapping in their characters. There is practically no character representative of any of the families, and they are rather traditional groupings of genera than related forms. The family Melanconidaceae is fairly constant, containing those genera of the Diaporthaceae with open conidial layers. The genus Diaporthe, however, is placed in the Valsaceae, while Endothia and Sillia are placed in the Melogrammataceae. Of the genera of the Allantosphaeriaceae, Diatrype, Quaternaria, and Diatrypella are placed in the Diatrypaceae, Anthostoma as a genus of the Valsaceae, and the rest under Valsa as subgenera. Euvalsa, Leucostoma, and Valsella, which, as we have seen, belong to the Diaporthaceae, are also placed as subgenera of Valsa. It will be noticed that Lindau's list of genera includes a number not considered by the writer. Many of these are genera segregated or indefinitely differentiated from those discussed. Others are small genera, material of which

was not available to the writer. Later studies of such genera will determine their true position in the general scheme here presented.

The recognition by von Höhnelt of the two large groups, the Allantosphaeriaceae and the Diaporthaceae, was a long step in advance over all previous classifications.

The writer's results have pointed to relationships which follow the general outlines put forth by von Höhnelt. The chief changes which are suggested are as follows:

1. The union of the genera *Cryptovalsa* and *Diatrypella*, since they are merely arbitrarily separated portions of the same line of development, differing only in degree of stromatic development.

2. The inclusion of the genera *Endoxyla*, *Anthostoma*, and certain species of *Valsaria* in the Allantosphaeriaceae, for reasons already stated.

3. The placing of *Endothia* in the Valsaceae, on account of the character of its conidial stage and because of the presence of allantoid ascospores in two species. The position of *Valsaria* in the Valsaceae is more or less questionable until further evidence is accumulated.

4. The inclusion of *Melanconis* and *Pseudovalsa* in the Diaporthaceae, since they show a distinct phylogenetic relationship to Diaporthe.

PROVISIONAL DESCRIPTION OF GENERA

The following generic descriptions are given in an attempt to circumscribe the genera studied on the basis of the phylogenetic relationships already discussed. In some cases the evidence is as yet inadequate for any final separation of generic groups. In such cases (as in *Eutypa*) a wide range of forms have been included in a single genus. The writer realizes that such groupings present a composite genus, and will necessarily call for rearrangement as our knowledge of life histories progresses. The following descriptions, however, are merely provisional, and given to present more clearly the preliminary outlines of the phylogeny of this group.

ALLANTOSPHAERIACEAE v. H.

Asci with more or less elongated, tapering, persistent stalks, resulting in a persistent, definite hymenial layer of asci. Paraphyses present but usually evanescent at maturity. Ostioles characteristically sulcate, except in *Anthostoma*. Asci 8- to many-spored. Ascospores allantoid to cylindrical or inequilateral-elliptical, one- to many-celled, yellowish hyaline to brown.

Conidia long-cylindrical to filiform, curved or hamate, and one-celled, borne in exposed layers, open cavities, enclosed locules, or labyrinthiform chambers (on free conidiophores in *Eutypa*). Either ectostromatic or entostromatic.

Eutypa Tul.

Stroma effuse; perithecia separately erumpent. Ectostroma not strongly developed, or absent. Ostioles punctate to sulcate. Ascospores biseriate, allantoid, yellow-hyaline, one-celled.

Imperfect stage ectostromatic, entostromatic, or hyphomycetous.

Cryptosphaeria Grev. *emend.*

Stromata effuse or isolated; perithecia separately or collectively erumpent, usually surrounded by a dark marginal zone. No mechanical ectostroma formed. Asci 8-spored. Ascospores irregularly biserial, allantoid to cylindrical, brown, one- to many-septate, often constricted. Filiform paraphyses present, and more or less persistent.

Imperfect stage entostromatic, forming labyrinthiform locules, so far as known.

Since the type species of Greville's *Cryptosphaeria* (*C. millipunctata*) has septate ascospores, and since, according to the scheme here presented, the other species of *Cryptosphaeria* would fall in either *Eutypa* or *Euanthostoma*, the name *Cryptosphaeria* is retained for those species with septate brown ascospores.

The species of *Valsaria* with obviously allantoid spores are placed here. It may be found advisable later to erect a new genus for these species with clustered perithecia.

Quaternaria Tul.

Entostroma effuse, but perithecia in small collectively erumpent clusters of 2-4. Spores biserial, allantoid, one-celled, yellow-brown.

Imperfect stage ectostromatic (*Libertella*).

This genus would differ from *Eutypa* only in its collectively erumpent perithecia, and would include some species usually placed in that genus. It would differ from *Eutypella* only in its ectostromatic conidial stage.

Diatrype Fr. *emend.*

Stroma effuse or isolated. Ectostroma strongly developed and deciduous. Entostroma forming a widely erumpent disc; dark marginal zone present. Perithecia lying parallel and separately erumpent. Ostioles sulcate. Asci 8-spored. Spores biserial, allantoid, one-celled, yellow-hyaline.

Imperfect stage ectostromatic.

Diatrypella Ces. & de Not. *emend.*

Stroma effuse or isolated. Ectostroma absent or strongly developed, but not deciduous. Entostroma well developed, often pustulate but usually not widely erumpent, bounded by a dark marginal zone. Perithecia usually clustered, rarely separately erumpent. Ostioles usually sulcate. Asci long-stalked, polysporous. Spores allantoid, one-celled, yellow-hyaline.

Imperfect stage primarily ectostromatic.

Diatrypella and *Cryptovalsa* Ces. & de Not. are here included under one genus, since they represent merely arbitrarily chosen portions of the same line of development and show no sharp line of demarcation.

Eutypella Nit.

Stroma effuse or isolated. Perithecia clustered and collectively erumpent (in some species some of the perithecia are sometimes separately erumpent). Ectostroma limited in development, usually in isolated patches. Entostroma often well developed and pustulate, surrounded by a dark

marginal zone. Ostioles sulcate. Asci 8-spored. Spores biseriata, allantoid, one-celled, yellowish to brownish-hyaline.

Imperfect stage entostromatic (Cytosporina).

Anthostoma Nit. emend.

Stroma effuse or isolated. No ectostromatic development. Perithecia separately erumpent (Euanthostoma), or clustered and collectively erumpent (Lopadostoma). Entostroma often strongly developed and serving to burst open the periderm, with or without a dark marginal zone. Ostioles irregularly sulcate or merely punctate. Asci cylindric-clavate to cylindrical, short-stalked, 8-spored. Spores irregularly biseriata to uniseriate, brown, allantoid to cylindrical or usually inequilaterally elliptical, one-celled. Paraphyses numerous and persistent.

Imperfect stage entostromatic (so far as known).

This description would include the dark-spored forms of *Cryptosphaeria*, e.g., *C. vicinula*.

DIAPORTHACEAE v. H.

Asci with short, evanescent stalks, soluble in water, resulting in a loose mass of free asci and spores within the perithecium except in those cases in which the asci are held in position by numerous paraphyses. Asci usually with a protoplasmic ring in the thickened tip. Paraphyses present; sometimes few and evanescent; sometimes numerous and persistent. Ascospores variable; elliptical, fusoid, allantoid, or long-cylindrical, one- to many-celled, hyaline or colored.

Imperfect stage various. Mostly with two types of conidia; one of which is short-cylindrical to filiform, curved or hamate, hyaline and one-celled, while the other may be elliptical, fusoid, long-cylindrical to clavate, one- to many-celled, or hyaline to brown. Conidia borne in exposed layers, open cavities, enclosed locules, or labyrinthiform chambers. Either ectostromatic or entostromatic.

Diaporthe Nit. emend.

Stromata effuse or isolated. Entostromatic areas more or less differentiated and light in color. A blackening of the substratum always present, either on the surface of the substratum or as a marginal zone about the entostromatic areas. Paraphyses few and evanescent. Ascospores elliptical or fusoid, hyaline, 2-celled, sometimes appendiculate.

Imperfect stage belonging to the form genus *Phomopsis*. Conidia of two types, produced within enclosed locules which are usually surrounded by a wall-like zone of dark-colored cells. Ectostromatic or entostromatic. One type of conidium cylindrical or elongate-fusoid to filiform, curved or hamate, hyaline, and one-celled; second type elliptical to fusoid, hyaline, and one-celled.

The present species of *Diaporthe* which would not be included under this description would fall within the genera *Melanconis* and *Pseudovalsa* as subsequently described.

Melanconis Tul. emend.

Stromata, so far as known, isolated. Disc consisting of a well developed conical ectostroma. Perithecia arranged circinately in the unaltered bark

tissue. No entostromatic development apparent, and no dark zone present. Paraphyses present; sometimes fairly numerous and persistent. Ascospores biseriate to uniseriate, elliptical, 2-celled, hyaline or brown, sometimes appendaged.

Imperfect stage belonging to the form genus *Melanconium*. Hymenial layers formed over the entire surface, or within cavities upon the flanks of a conical or pulvinate ectostroma. Conidia of two types, at least in some species: one, small, cylindrical to elliptical, one-celled, and hyaline; the second, larger, elliptical to fusoid, one-celled, and colored.

Pseudovalsa Ces. & de Not. *emend.*

Stromata effuse (?) or isolated. Ectostroma not sharply differentiated; stromatic development usually entostromatic. Perithecia irregularly scattered or clustered. Entostromatic tissue usually dark-colored, not light in color as in *Diaporthe*. Irregular darkened marginal zones present in some species. Ascospores biseriate, two- to many-celled, hyaline or brown, sometimes appendaged.

Conidia borne in enclosed locules, shallow cavities, or exposed layers, within or upon an ectostromatic tissue. Conidia of two types: one, small, long-cylindric to allantoid, curved or hamate, hyaline, one-celled; the second, larger, elliptical to clavate or elongate, hyaline or brown, one- to many-septate.

The above description has been made general enough to include all forms hitherto reported with septate conidia. As has been pointed out, the evidence for such a grouping is as yet insufficient, and further cultural connections are needed either to confirm or to alter these relationships.

Mazzantia Mont.

Stroma isolated. Entostroma differentiated, light in color, bounded by a darkened marginal zone. Ascospores one-celled, elliptical, hyaline.

Conidia cylindrical, hyaline, one-celled, within enclosed locules.

Further study may show it advisable to unite this genus with *Diaporthopsis* into a genus corresponding to *Diaporthe* but with one-celled ascospores.

Diaporthopsis Fabre

Stromata effuse. Entostromata differentiated, light in color, bounded by a dark marginal zone. Ascospores one-celled and hyaline.

Cryptosporella Sacc.

Stromata isolated. Ectostroma forming a small conical disc. Entostroma not developed; perithecia buried in the unaltered bark; no marginal line present. Ascospores elliptical to fusoid, hyaline, one-celled.

Conidia elliptical to fusoid, hyaline, one-celled, produced in more or less open cavities or locules within an ectostroma. Sometimes a second type of smaller, cylindrical or filiform, curved, hyaline, one-celled conidia.

Cryptospora Tul. *pro parte*

Stromata as in *Cryptosporella*. Ascospores long-cylindrical, hyaline, one-celled or faintly septate (Sillia).

Conidia elongate-fusoid or cylindrical, borne in open cavities or layers within an ectostroma. Sometimes a second type of smaller, filiform or cylindrical, curved, hyaline, one-celled conidia.

Valsa Fr. *pro parte* (section *Euvalsa* Nit.)

Stromata isolated. Perithecia clustered in the unaltered bark tissues beneath a distinct conical ectostroma. No marginal zone present. Ascospores allantoid, one-celled, hyaline. Asci 8-spored.

Pycnidia (*Cytospora*) entostromatic, containing numerous coalescent locules forming a labyrinthiform chamber. Conidia allantoid, one-celled, hyaline.

Leucostoma Nit. (section)

Stromata isolated or confluent. Each perithecial cluster enclosed by a dark marginal zone, within which there is a strong development of entostromatic hyphae. Perithecia imbedded within this differentiated entostroma. Asci 8-spored. Ascospores allantoid, hyaline, one-celled.

Pycnidia and conidia as in *Valsa*, but with a somewhat greater stromatic development.

Valsellà Fck.

Same as *Leucostoma*, except that the asci are many-spored.

Endothia Fr. (sense of Shear)

Stromata isolated or confluent. Entostroma strongly developed, colored, without any marginal zone. Ascospores biseriata, allantoid to elliptical, hyaline, one- or 2-celled.

Pycnidia consisting of numerous locules which often coalesce to form a labyrinthiform chamber, formed within either ectostromatic or entostromatic tissue. Conidia small, elliptical to cylindrical, hyaline, one-celled.

Valsaria Ces. & de Not. *pro parte*

Stromata isolated or confluent. Practically no ectostromatic development. Entostroma very strongly developed, often erumpent, bounded by a dark marginal zone, usually colored. Paraphyses numerous and persistent. Ascospores uniseriate, elliptic-fusoid, 2-celled, brown.

Pycnidia consisting of numerous or labyrinthiform locules within the entostroma. Conidia small, elliptical, one-celled, hyaline.

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